University of Alberta

From cutblock to landscape: Site-specific and landscape-scale responses of songbirds to forest harvesting.

by

Michael Robert Norton ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring 1997

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ***From cutblock to landscape: Site-specific and landscape-scale responses of songbirds to forest harvesting*** submitted by ***Michael Robert Norton*** in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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There is a kind of indeterminacy...
which lies in the fact that we can neither consciously sense
nor think
of very much at any one moment.
Understanding can only come from a roving viewpoint
and sequential changes in the scale of attention.

- C.S. Smith

As the crickets' soft autumn hum
is to us
so are we to the trees
as they are
to the rocks and hills.

- Gary Snyder

ABSTRACT

Industrial logging in northern Alberta's boreal forest may threaten many songbird species. I studied two questions related to the effects of logging on songbirds. At a site-specific scale, I investigated the response of songbirds to partial-cut logging relative to clearcut logging. I found that increased retention of live trees on cutblocks helped maintain bird communities at conditions closer to pre-harvest. Birds in tree- and shrub-dependent guilds benefitted the most from partial-cutting. At a landscape scale I investigated the importance of spatial perspective on our interpretation of fragmentation effects by adopting a multi-scale approach to sampling in two 7000 ha landscapes, one of which had been fragmented by clearcut logging. An analysis of aspen (*Populus tremuloides*) patches in a wider landscape context than a simple patch-centred view changed the apparent response of several bird species to landscape fragmentation. Similarly, sampling conducted at different spatial scales showed different patterns. Little evidence was found for inherent thresholds of scale within either landscape. I advocate multiple scales of analysis and a broader view of boreal systems than a 'patch-centred' perspective to adequately assess effects of fragmentation.

ACKNOWLEDGEMENTS

I have waited a long time to write what I thought would be the easiest and most enjoyable section of my thesis. Most enjoyable maybe, but definitely not the easiest. More people than I can name here have helped in the completion of this tome over the last 2½ years or so. I will name a few here, and to the others: you'll just have to believe me that I have indeed appreciated your input.

I cannot possibly thank anyone other than Susan Hannon first. She has been involved in all stages of brain-bruising, from poring over harvest maps to working through the statistical mess that became Chapter 3, but always giving me the space to figure out how to do it on my own. The independence I have learned will be one of the best lessons of graduate school.

I am truly indebted to the various friends, as they became, who helped me in the field: Ben Olsen, Mark Hebblewhite, Mick Panesar, and especially Marg Lomow. All of them put in more effort than I could reasonably ask for, drove more bone-jarring miles on a quad than I thought humanly possible, got up before dawn too many times (long live the Bodum!), and put up with warm beer on top of it all. Marg was my lifeline to sanity during my first, very hectic, field season. Thanks for putting up with me (and the mud, and the bugs...). And what can I say about Cindy McCallum that hasn't already been said? The most cheery (infernally so at 4 am), organized and devoted technician you could ask for, and more.

My time in grad school was enriched by all of the others in the Ecology group for all the various discussions, academic and otherwise. Thanks especially to Craig Machtans for always responding to queries through the bookshelf of "Hey Craig, you got a minute?" To all those who I have pestered for statistical advice: thanks, you were a 'significant' help.

To my parents, whose unfaltering support and encouragement have kept me going through my almost 8 years (yikes!) of university, this thesis proves you were right: I *can* do it, and it *is* worth it. In the same vein I should thank `javery@morgan.ucs.mun.ca`, who I could always count on for support and smiles whenever I needed them.

And lastly to Kim. I can't possibly express my love and gratitude to you here, but I can offer one thought which should make you smile: IT'S DONE!

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CHAPTER 1

Thesis Introduction

1.1 Research Background

A suspicion that several species of songbirds were on the decline in eastern North America was confirmed in the late 1980's with a detailed analysis of breeding bird survey records (Robbins *et al.* 1989*b*, Askins 1993). Hypotheses to explain the declines in eastern populations have pointed to human-induced habitat alteration through expansion of agriculture, urban areas, forestry, and other industrial land-uses. Populations of Neotropical migrant species are dwindling more rapidly than their short-distance migrant and non-migratory counterparts, likely the result of a combination of causes on their wintering grounds and stop-over habitat in addition to problems in summer breeding areas (Terborgh 1989, Moore and Simons 1992, Böhning-Gaese *et al.* 1993, Rappole and McDonald 1994). Population declines are less evident in western parts of the continent (Sauer and Dreoge 1992, Peterjohn and Sauer 1994) possibly because a greater proportion of breeding habitats remain intact there.

The boreal forest of northern Alberta provides breeding habitat for roughly 95 species of songbirds (Passeriformes) of which 48 are long-distance migrants (Smith 1993). Although the majority of Alberta's boreal forest still exists in its natural state, this region is under heavy pressure from industrial forestry operations and current provincial government policy which aims to lease the majority of merchantable timber areas to logging companies. Trembling aspen (*Populus tremuloides*) stands are now also considered an economically viable source of fibre, and there has been a great increase in the demand for this species in the last decade. Current operating ground rules for forest harvest specify a two or three pass clearcutting system whereby equal amounts of timber are taken from a given area in each of two or three harvesting periods spaced at roughly 10 year intervals (Anonymous 1992). The accompanying habitat loss and large scale alteration of landscape patterns (Franklin and Forman 1987) have the potential to exacerbate problems already faced by songbird populations.

Possible problems of clearcut logging for songbirds can be broadly classified into

two categories: (1) those associated with loss of mature and old forest habitats, and (2) the fragmentation of remaining forest areas into smaller, spatially separated patches. Although the result of these classes of problems may be the same (further declines in songbird populations), from a forest management standpoint they may require quite distinct plans for amelioration. Some aspects of the habitat loss problem can be approached from the level of the individual cutblock, whereas landscape fragmentation must be dealt with at much larger spatial scales.

The short-term, local-scale effects of aspen clearcutting are well-established. Essentially, removal of forest canopy causes a decline in the number of forest-dwelling bird species and an increase of birds characteristic of more open habitats (DeByle 1981, Scott and Crouch 1987, 1988). Bird communities appear to change in a manner which tracks the regenerating forest (Crawford *et al.* 1981, Welsh 1987, Westworth and Telfer 1993). The initial loss of forest species is usually attributed to a lack of the vegetation structure necessary for nesting and foraging.

There are various forms of partial-cut logging that could lessen the impacts on birds. Vegetation structure, which is retained on site, could provide sufficient habitat for forest species such that there would be a smaller community shift after logging (Thompson *et al.* 1993). Responses of birds to partial-cutting have not been well investigated, but there are likely to be differential responses by individual species and by foraging and nesting guilds. Species which nest or forage in the canopy are likely to be more affected affected by harvesting than species in ground-dwelling guilds (Medin and Booth 1989). Longer-term responses to retained vegetation have not been documented. The reduced community shift could help speed the process of recovery of bird communities to pre-harvest levels. However, the large amount of edge habitat created could lead to increases in nest predation and parasitism rates. Parasitism rates by Brown-Headed Cowbirds (*Molothrus ater*) have been found to increase in forest openings as small as 0.2 ha (Brittingham and Temple 1983), a size comparable to small openings from group-selection logging (Thompson *et al.* 1993).

The processes by which landscape fragmentation acts to reduce bird numbers and

productivity have been studied in much more detail. Effects of reduced habitat area and isolation of habitat patches on bird species richness are usually interpreted through island biogeographic theory (MacArthur and Wilson 1967) and metapopulation theory (Levins 1970). The principal difference between these theoretical approaches lies in the assumption of the presence of a "mainland" source of dispersing individuals in the former, but not the latter. While there have been many theoretical and conceptual variations on the theme of local extinction and recolonization rates (*e.g.* Harrison 1991), the community patterns which can be expected from both island biogeographic and metapopulation processes are superficially similar. Smaller habitat areas are able to support fewer species, and spatial separation of patches reduces the ability of new individuals to colonize those patches, leading to community relaxation. Additionally, bird productivity in habitat fragments may be lower as a result of increased nest predation or parasitism (Paton 1994, Andrén 1995), or through changes in microclimate (Saunders *et al.* 1991) which may affect forage availability. These sorts of indirect effects of fragmentation can also threaten the long-term viability of populations and communities in forest fragments.

Most studies of birds in fragmented habitats have been conducted within a particular habitat patch type at one arbitrary spatial scale (*e.g.* Blake and Karr 1984, Lynch and Whigham 1984, Freemark and Merriam 1986, Blake and Karr 1987, van Dorp and Opdam 1987, Robbins *et al.* 1989*a*), although there are some notable exceptions (*e.g.* Virkkala 1991). Results from these and other studies are being applied to the management of forestry practices (Schmiegelow and Hannon 1993). Caution must be exercised in making such extrapolations, however, because there is a rapidly growing body of evidence which shows that ecological patterns and processes observed at one scale may not be directly transferable to other larger scales (Wiens 1989, May 1994, Turner *et al.* 1995). Local species extinctions may be the result of larger scale spatial redistributions and not population declines *per se*. As well, unlike the situation in agriculture-dominated ecosystems, forest habitat patches frequently do not exist as isolated 'islands' and may influence, and be influenced by, other habitat elements in the surrounding matrix (Wiens 1994).

In this thesis I present the results of two studies which relate to each of the aforementioned classes of concerns with clearcut logging. In Chapter 2 I report on a study which investigated the short-term responses of songbirds to partial-cut logging as compared to clearcut logging. Three different levels of vegetation retention on cutblocks are compared to uncut forests in an experimental setting to assess their relative impacts on bird communities. In Chapter 3 I present the results of a study which dealt with the issue of spatial scale in the applied context of forest fragmentation. The significance of the usual study design for carrying out research in fragmented landscapes is examined by comparing the results obtained at a 'typical' spatial scale to those obtained over a larger spatial scale. In that chapter I also assess the effects of viewing habitat patches in a larger landscape context, rather than as simple 'islands'. I conclude the thesis with Chapter 4 in which I summarize some of the main findings and implications of the studies presented in the middle two chapters, and suggest some directions for future research into those areas.

1.2 Literature Cited

Anonymous. 1992. Timber harvesting planning and operation ground rules. Alberta Energy/Forestry, Lands and Wildlife Publ. No. 67. Edmonton. 75 pp.

Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. pp. 225-255 in: L. Hansson, L. Fahrig, and G. Merriam, eds. *Mosaic landscapes and ecological processes*. Chapman & Hall: London, UK.

Askins, R.A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. pp. 1-34 in: D.M. Power, ed. *Current Ornithology*. Volume 11. Plenum Press: New York, NY.

Blake, J.G. and Karr, J.R. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. Biol. Conserv. **30**:173-187.

Blake, J.G. and Karr, J.R. 1987. Breeding birds of isolated woodlots: Area and habitat relationships. Ecology **68**:1724-1734.

Böhning-Gaese, K., Taper, M.L., and Brown, J.H. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conserv. Biol. 7:76-86.

Brittingham, M.C. and Temple, S.A. 1983. Have cowbirds caused forest songbirds to decline? BioScience **33**:31-35.

Crawford, H.S., Hooper, R.G., and Titterington, R.W. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. J. Wildl. Manage. **45**: 680-692.

DeByle, N.V. 1981. Songbird populations and clearcut harvesting of aspen in northern Utah. Res. Note INT-302. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Franklin, J.F. and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecol. **1**:5-18.

Freemark, K., and H.G. Merriam. 1986. The importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. **36**:115-141.

Harrison, S. 1991. Local extinction in a metapopulation context: An empirical evaluation. Biol. J. Linn. Soc. **42**:73-88.

Levins, R. 1970. Extinction. pp. 77-107 in: M. Gerstenhaber, ed. *Some mathematical questions in biology*. Lectures on mathematics in the life sciences, Vol. 2. American Mathematical Society, Providence, RI.

Lynch, J.F., and Whigham, D.F. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biol. Conserv. **28**:287-384.

MacArthur, R.H., and Wilson, E.O. 1967. The theory of island biogeography. Princeton Univ. Press: Princeton, NJ. 203 pp.

May, R.M. 1994. The effects of spatial scale on ecological questions and answers. pp. 1-17 in: P.J. Edwards, R.M. May, and N.R. Webb, eds. *Large scale ecology and conservation biology*. Blackwell Scientific Publications: Oxford, UK.

Medin, D.E., and Booth, G.D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. Res. Pap. INT-408. USDA Forest Service Intermountain Research Station, Ogden, UT. 11 pp.

Moore, F.R., and Simons, T.R. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. pp. 345-355 in: J.M. Hagan and D.W. Johnson, eds. *Ecology and management of Neotropical migrant landbirds*. Smithsonian Inst. Press: Washington D.C.

Paton, P.W.C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conserv. Biol. **8:**17-26.

Peterjohn, B.G. and Sauer, J.R. 1994. Population trends of woodland birds from the North American Breeding Bird Survey. Wildl. Soc. Bull. **22:**155-164.

Rappole, J.H. and McDonald, M.V. 1994. Cause and effect in population declines of migratory songbirds. Auk **111:**652-660.

Robbins, C.S., Dawson, D.K., and Dowell, B.A. 1989*a*. Habitat area requirements of breeding forest birds of the middle Atlantic States. Wildl. Monogr. **103:**1-34.

Robbins, C.S., Sauer, J.R., Greenberg, R.S., and Droege, S. 1989*b*. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. USA **86**: 7658-7662.

Sauer, J.R. and Droege, S. 1992. Geographic patterns in population trends of Neotropical migrants in North America. pp. 26-42 in: J.M. Hagan and D.W. Johnson, eds. *Ecology and management of Neotropical migrant landbirds.* Smithsonian Inst. Press: Washington D.C.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: A review. Conserv. Biol. **5**:18-32.

Schmiegelow, F.K.A, and Hannon, S.J. 1993. Adaptive management, adaptive science and the effects of forest fragmentation on boreal birds in northern Alberta. Trans. N.A. Wildl. and Natur. Resour. Conf. **58:**584-598.

Scott, V.E., and Crouch, G.L. 1987. Response of breeding birds to commercial clearcutting of aspen in southwestern Colorado. Res. Note RM-475. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Scott, V.E., and Crouch, G.L. 1988. Breeding birds in uncut aspen and 6- and 10-year-old clearcuts in southwestern Colorado. Res. Note RM-485. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Smith, A. 1993. Ecological profiles of boreal forest birds in western and northern Canada. pp. 14-26 in: D. Kuhnke, ed. *Birds in the boreal forest: Proceedings of a workshop held March 10-12 in Prince Albert, SK.* Forestry Canada and Environment Canada, Edmonton, AB.

Terborgh, J. 1989. Where have all the birds gone? Princeton Univ. Press: Princeton, NJ.

Thompson, F.R, Probst, J.R., and Raphael, M.G. 1993. Silvicultural options for Neotropical migratory birds. pp. 353-362 in: D.M. Finch and P.W. Stangel, eds. *Status and management of Neotropical migratory birds.* Gen. Tech. Rep. RM-229. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Turner, M.G., Gardner, R.H., and O'Neill, R.V. 1995. Ecological dynamics at broad scales. BioScience **45:**S29-S35.

van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecol. **1:**59-73.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: A multi-scale approach. Oikos **62:**59-66.

Welsh, D.A. 1987. The influence of forest harvesting on mixed coniferous-deciduous boreal bird communities in Ontario, Canada. Acta Oecologia **8**: 247-252.

Westworth, D.A., and Telfer, E.S. 1993. Summer and winter bird populations associated with five age classes of aspen in Alberta. Can. J. For. Res. **23**: 1830-1836.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecol. **3**:383-397.

Wiens, J.A. 1994. Habitat fragmentation: Island *v* landscape perspectives on bird conservation. Ibis **137**:S97-S104.

CHAPTER 2

Songbird response to partial-cut logging in the boreal mixed-wood forest of Alberta.[1]

2.1 Introduction

Population declines in several species of birds, particularly Neotropical migrants, have been attributed to the destruction of their breeding habitat by human activities (Whitcomb *et al.* 1981, Robbins *et al.* 1989, Morton 1992), including logging. Short term effects of clear-cutting are well documented (*e.g.* Franzreb and Ohmart 1978, Crawford *et al.* 1981, Thompson *et al.* 1992) and several studies have documented extensive shifts in bird communities as the forest regenerates (*e.g.* Welsh 1987, Westworth and Telfer 1993). The long term impacts of clearcutting are not known, however.

Selective and partial-cutting techniques are frequently cited as less invasive alternatives to clearcutting, particularly by many of the public who view clearcutting as an inferior and overly destructive harvesting procedure (*e.g.* Devall 1993). Little is known, however, of the impact of partial-cutting techniques on wildlife (but see Freedman *et al.* 1981, Scott and Gottfried 1983, Medin and Booth 1989). Partial-cutting retains vegetation structure that could reduce the magnitude of change in bird communities compared to even-aged management such as clearcutting (Thompson *et al.* 1993). On the other hand, the large amount of edge habitat created by partial-cut logging could negatively affect songbirds through increased nest predation or brood parasitism rates associated with forest edges (Wilcove 1985, Thompson 1993). Also, if disturbed sites function as suboptimal habitat for some forest-dwelling birds, the reproductive potential of many birds inhabiting partial-cuts might be lower than in undisturbed forest. Potential benefits still suggest, though, that partial-cutting may be a useful tool in multiple-landuse management when implemented in concert with other harvesting strategies and landscape-

[1] A version of this chapter was accepted for publication in *Canadian Journal of Forest Research* on September 10, 1996. The version included in this thesis is identical to the published form except the abstract has been removed, a section titled "Management Considerations" has been added, and a few minor grammatical changes have been made. Norton, M.R. and Hannon, S.J. In Press. Songbird response to partial-cut logging in the boreal mixed-wood forest of Alberta. Can. J. For. Res.

scale planning (Mladenoff *et al.* 1994).

In this chapter I report on a two-year study of partial-cutting in the boreal mixed-wood forest of north-central Alberta. I evaluated the effects on songbirds of two levels of partial-cut logging, relative to structured clearcuts and unharvested sites. Bird communities, guilds and species in all harvested treatments were compared to unharvested areas to evaluate whether any of the treatments had similar bird communities as found in unharvested areas. I predicted that the partial-cut sites with more residual material would support bird communities that were more similar to uncut forest than traditional clearcut harvesting, but speculated that the impact of logging activity in partial-cut sites was likely to be high enough to cause significant shifts in community structure. I also predicted that guilds and species more explicitly dependent on tree and shrub layers would show the greatest differences among harvesting treatments.

2.2 Methods

2.2.1 Study site and experimental design

The study was conducted in an area (approximately 10 km by 10 km) near Calling Lake, Alberta (55° 15' N, 113° 35'W) in boreal mixed-wood forest. Forest cover in this area has been little reduced by logging to date so the study area can be viewed as a disturbed site within an otherwise mostly contiguous forested landscape. Forest stands in the area are pyrogenic and are dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). White spruce (*Picea glauca*) is scattered through predominantly hardwood stands, and patches of black spruce (*P. mariana*) and bogs are interspersed across the landscape. Understorey vegetation is dominated by wild rose (*Rosa* spp.) and alder (*Alnus crispa* and *A. tenuifolia*). All stands chosen for this study were at least 130 years old according to forest inventory maps.

Three stands within each of 3 harvesting treatments (structured clearcut and two levels of partial-cut: low residual vegetation and high residual vegetation) were chosen from an existing harvest plan of Alberta-Pacific Forest Industries (Boyle, Alberta). In addition, 3 unharvested controls were chosen in the same area. Harvesting treatments were interspersed, but control sites were clustered together in the only accessible region of

equivalent uncut forest. Because cutblocks varied in size, each treatment had a replicate of approximately 11, 22 and 29 ha in size (Fig. 1). We chose stands with similar amounts of white spruce and nonmerchantable timber, and which were adjacent only to similar old hardwood stands, and not to bog or conifer stands. All blocks were at least 400 m apart, and all control sites were at least 800 m from the nearest harvested area. Baseline (precut) data were gathered during the summer of 1994, harvesting was conducted during the winter of 1994-95, and post-cut data were collected during the summer of 1995. Harvesting was accomplished with the same equipment often used in conventional clearcut logging: feller-bunchers, skidders, and roll-stroke delimbers. In all harvested blocks a central yarding area ranging from 10 - 50 m wide was cleared for delimbing and loading, and the remainder of each cutblock was partially cut. Logging operators were instructed to leave vegetation in intact patches wherever possible, and to leave patches evenly distributed over each cutblock without preference for timber type. After harvesting, partial-cuts had roughly 30% and 40%, respectively, of the original vegetation cover (tall shrub, subcanopy, and canopy) remaining, after removing the road allowance. Retention approaching 50% is probably the upper limit for this type of logging.

2.2.2 Vegetation data

Vegetation data were collected at all sites in 1994 before harvesting based on a modified version of the protocol of Martin (1992). Three 0.04 ha circular plots were surveyed at each point count station, with plots located 30 m from the station at angles of 0°, 120° and 240°. The following data were collected: percent ground cover was estimated for 7 vegetation classes (all green, forb, low shrub[<1 m], grass, moss/fern, coarse woody debris [downed woody material ≥ 5 cm diameter], leaf litter) in four 1 m^2 quadrats per plot; number of stems for each shrub species was determined in the same 4 quadrats; number of small trees (<2.5 cm and 2.5 - 8.0 cm diameter at breast height [dbh]) by species in 0.008 ha sub-plots; number of trees by species in 4 dbh classes (8-15, 15-23, 23-38, >38 cm) in the total plot; number of snags 8-12 cm dbh in the total plot; species, height and dbh of snags > 12 cm dbh in the total plot; heights of the canopy, subcanopy and tall shrub layers (measured with a clinometer); and canopy cover (measured with a

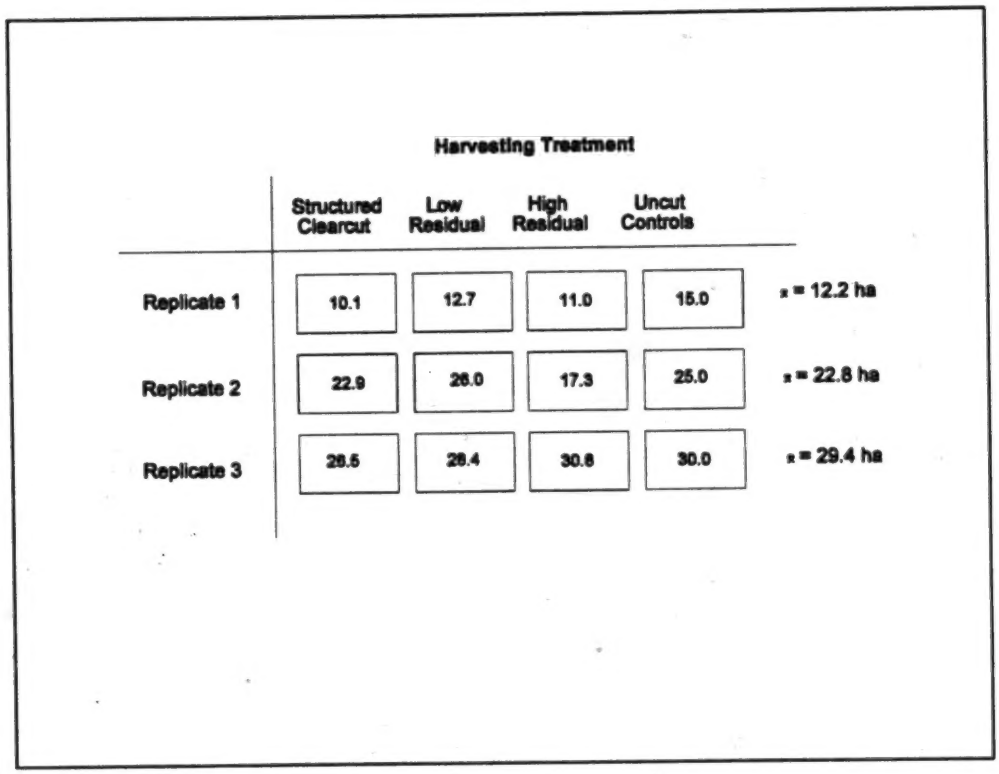

Figure 2-1: Schematic representation of experimental design showing three replicates of four treatments. Actual sizes of individual cutblocks are given in hectares inside the boxes; mean cutblock size for each replicate is shown.

spherical densiometer).

Eleven principle variables from the three vegetation strata (canopy, tall shrub, ground) were compared among treatments (Table 1). The data did not conform to the assumptions necessary for a multivariate ANOVA (normality and homoscedasticity, Scheiner 1993), even after transformation. Therefore, each variable was compared among treatments using Kruskal-Wallis ANOVA. A Bonferroni sequentially corrected significance level (Rice 1989) was used to assess differences between treatments.

The amount of residual vegetation remaining in the blocks after harvesting was quantified from 1:20000 aerial photographs. Residual patches of trees and tall shrubs, and large individual trees were identified and mapped at 1:15000 using an 8 power magnification CP1 stereo aerial photo viewer with attached pantograph. The measure of retained vegetation cover therefore included canopy and subcanopy trees, and patches of tall shrubs (hereafter simply called vegetation cover). Maps were converted to black/white cover diagrams which were subsequently scanned into SPANS© Geographic Information System software package for analysis of patch areas. The area of each road allowance was calculated. Total residual vegetation coverage was calculated and broken down into 3 size classes of residual patches. These were < 0.03 ha, representing groups of very few trees and individual stems, 0.03 - 0.1 ha, representing small patches likely to have no intact understorey (based on field observations), and > 0.1 ha to include large patches with an intact shrub and ground layer. The contribution of each patch size class to the total residual vegetation area was analyzed using Kruskal-Wallis ANOVA to determine if blocks with less residual vegetation contained a disproportionate amount of the total vegetation as very small groups of trees. Cover estimates from densiometer readings before logging were used to calculate the percentage of original vegetation cover which remained after logging, both including and excluding road clearances.

2.2.3 Bird census

Songbird communities were surveyed using a fixed-radius point-count technique following standards recommended by Ralph *et al.* (1993). A radius of 100 m was used because a smaller radius gave unacceptably small sample sizes. Blocks were sampled at an

intensity of approximately 1 census station per 5 ha, and stations were located 200 m apart; efforts were taken to minimize double-counting of birds at adjacent stations. We surveyed birds at the peak of the breeding season each year (late May to early July), from sunrise until 10:00 am. Trained observers were rotated among sites. Each station was visited 3 times in 1994 and 4 times in 1995 for 5 minutes per visit; only 3 census rounds of corresponding dates were used for between year comparisons. One or more registrations of a singing male over the 3-4 rounds was required to record the species as present in a site; simultaneous registrations of singing males were required to accept more than one pair at a given station. Total abundance (*i.e.* the number of presumed pairs) at a given station was calculated as the maximum number of individuals recorded for each species on a given visit to a station (Blondel *et al.* 1981, Blake *et al.* 1994). Singing males, observed pairs, and nests were scored as 1.0, silent or calling birds were scored as 0.5. Bird densities were not calculated because of the requirement of accurate distance estimates for each bird detection (Blake *et al.* 1994).

2.2.4 Bird data analyses

A *Q*-mode hierarchical cluster analysis was performed using a phi-square distance measure on pre-logging bird communities at all cutblocks, because several vegetation characteristics varied among sites before logging (see below: § 2.3.1 *Results: Vegetation characteristics of the blocks*). Ward's method was used to form clusters as it produces the tightest clusters (Kent and Coker 1992). If bird communities varied systematically among treatments before logging, treatments would cluster together in the resulting dendrogram.

Changes in species richness and total bird abundance between years in harvested sites relative to the control sites were assessed using a repeated measures ANOVA with contrasts. The effect levels of each treatment were compared with a one-way ANOVA on the difference in richness and abundance between years. Change in abundance was also regressed against the proportion of vegetation retained on each cutblock. To quantify differences in species composition between years, the Jaccard index was calculated for each block as a simple resemblance function for binary (presence-absence) data (Ludwig and Reynolds 1988). This index ranges from 0, for sites with no species in common, to 1

for identical community compositions. To incorporate information about species relative abundances as well as species identity, the Phi-square similarity measure was also calculated for each block. This index also ranges from 0 to 1 and is computed for frequency count data, and includes a correction for the total frequencies of the two sites being compared (Jackson *et al.*1989). The two indices were compared among treatments with a one-way ANOVA.

At a finer scale of resolution, bird species were grouped into guilds based on primary foraging or nesting habits (as identified by Ehrlich *et al.* [1988]). Nesting guilds considered were ground, tree/shrub, and cavity; foraging guilds were ground, foliage gleaning, and aerial/hover gleaning. The bark foraging guild contained too few species to analyze. Census stations within each block were combined to obtain larger sample sizes, and the number of stations was included as a covariate in analyses. Total bird abundances in each guild were compared (1) within a treatment between years and (2) across treatments within each year by ANCOVA with the number of census stations in each treatment as a covariate.

The equivalent comparisons were also completed at the level of individual species. Low residual and high residual treatments were combined for the species-level analyses because of small sample sizes and the similarity of the two partial-cut treatments' residual vegetation (see below, § 2.3.1 *Results: Vegetation characteristics of the blocks*). Tests were calculated for each species' abundance at each census station. Between-year comparisons within each treatment were calculated with Wilcoxon Matched-Pair Signed-Rank tests. Comparisons among treatments used a Kruskal-Wallis ANOVA on the difference in abundance between years of each species at each site.

All analyses were performed using SPSS™ release 6.1.

2.3 Results

2.3.1 Vegetation characteristics of the blocks

Several vegetation variables varied significantly among sites prior to harvest (Table 2-1). This appeared to be due to variation in the control sites in all cases. Of particular potential concern were the differences in deciduous stem density and snag density which

Table 2-1: Mean and standard deviation of vegetation characteristics on experimental cutblocks prior to harvest. Vegetation was measured at 3, 0.04 ha circular plots at each bird census station (n = 13 low residual, high residual; n = 14 clearcut, uncut).

	Clearcut	Low residual	High residual	Control	Significance[a]
Canopy					
Deciduous tree density[b]	416.7 (29.2)	411.5 (46.6)	373.6 (41.4)	269.1 (29.0)	0.008
Coniferous tree density[b]	26.8 (10.0)	17.9 (10.2)	28.5 (15.6)	68.5 (39.1)	0.897
Snag density[b]	66.7 (8.6)	63.1 (7.6)	72.9 (7.7)	102.7 (12.7)	0.081
Canopy cover (%)	72.4 (2.6)	69.2 (2.7)	66.5 (3.8)	65.2 (2.8)	0.396
Canopy height (m)	26.1 (1.0)	26.2 (1.3)	26.9 (0.6)	25.9 (1.1)	0.852
Tall shrub					
Alder/willow density[c]	974.1 (136.0)	959.7 (92.1)	1222.2 (187.1)	760.7 (124.8)	0.215
Deciduous sapling density[d]	165.6 (21.1)	152.9 (19.7)	224.0 (46.9)	211.8 (27.7)	0.372
Ground					
All green cover[e]	66.7 (3.2)	60.9 (2.8)	68.5 (2.2)	45.5 (2.7)	< 0.001
Low shrub cover[e]	38.2 (2.7)	33.7 (2.8)	37.0 (2.2)	20.2 (2.7)	0.001
Forb cover[e]	32.1 (3.6)	20.1 (1.3)	30.4 (3.1)	17.9 (1.1)	0.002
Moss cover[e]	2.8 (0.9)	3.3 (0.8)	2.9 (0.9)	2.8 (0.9)	0.738

[a] Determined by Kruskal-Wallis ANOVA with Bonferroni correction.
[b] Expressed as average number of stems/ha.
[c] Density of *Alnus crispa*, *A. tenuifolia*, and *Salix* spp. stems per ha.
[d] Density of *Populus tremuloides*, *P. balsamifera*, and *Betula papyrifera* stems per ha.
[e] Expressed as average percent cover within 1 m^2 plots.

were 32.8% lower ($H = 11.80$, $p = 0.008$) and 52.0% higher ($H = 6.73$, $p = 0.081$), respectively, in the controls than the other treatments, probably indicative that control stands were slightly older. There was also a trend towards a higher coniferous component in the controls. Although these differences are not significant by the sequential Bonferroni technique (Rice 1989), I felt that they might influence bird communities. However, a hierarchical cluster analysis of all sites pre-cutting based on bird communities did not suggest a difference in bird community structure at the control sites since those 3 sites did not form a distinct cluster (M. Norton, unpublished data).

After logging, cutblocks varied in terms of the actual amount of residual vegetation and its distribution over the blocks. Although the low and high residual treatments had quite similar amounts of retained vegetation ($\bar{x} = 25.0\%$ and 36.7%, respectively), they are statistically different ($U = 6.0$, $p = 0.05$) and were considered separately for most analyses. The clearcuts averaged only 6.7% vegetation retention. When road allowances were removed from consideration, retention levels were 8.5%, 30.1%, and 40.3%, respectively. The contribution to the total residual material of each of three size classes of residual patches were approximately equal among treatments (Fig. 2-2), and were not significantly different between treatments (< 0.03 ha, $H = 2.40$, $p = 0.30$; 0.03 - 0.1 ha, $H = 0.622$, $p = 0.73$; >0.1 ha, $H = 1.16$, $p = 0.56$) so there should have been no confounding effects from the patch size distribution in each treatment.

2.3.2 Species richness, abundance and turnover

There was a highly significant negative effect of harvesting on both species richness and bird abundance ($F = 46.77$, $p < 0.001$, Fig. 2-3). The control sites recorded increases of 47.4% in species richness and 50.7% in total bird abundance, whereas both parameters decreased in all harvested sites (contrasts, $p < 0.001$ in all cases). Post-cutting species richness per station was 61.2%, 43.4%, 25.3% lower than the controls (Fig. 2-3); bird abundances were 65.4%, 48.7%, and 30.0% lower than the controls, for clearcut, low residual and high residual treatments respectively. The magnitude of the declines on harvested sites was not significantly different between the low and high residual treatments for either parameter (Fig. 2-3), and the drop in species richness did not differ between

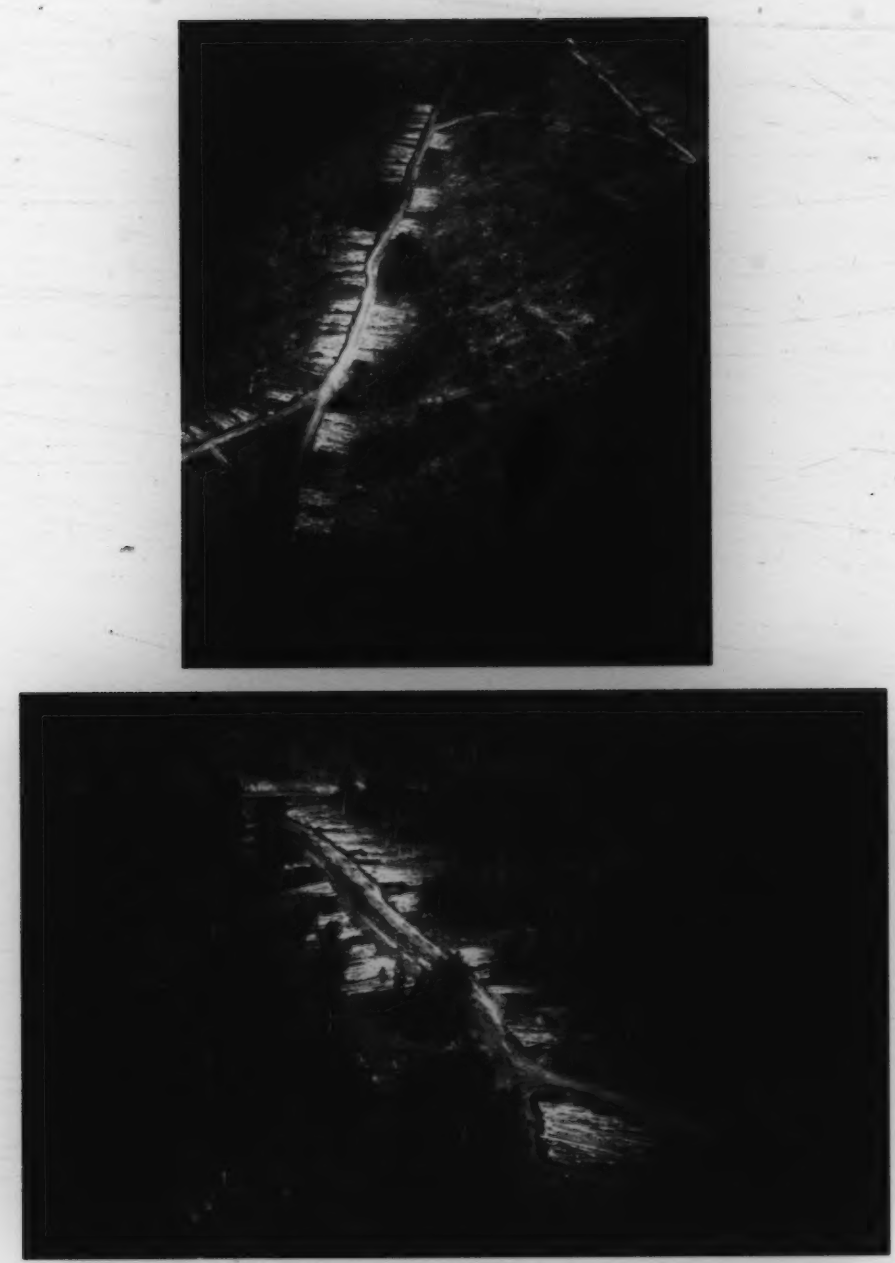

Figure 2-2: Representative examples of structured clearcut (top) and 30% partial-cut (bottom) logging. Photos show part of cutblocks of 32 ha and 14 ha, respectively. Note the distribution of residual live trees in various sized patches. The lower photo shows the central road which was cleared for delimbing and loading of logs in all cutblocks.

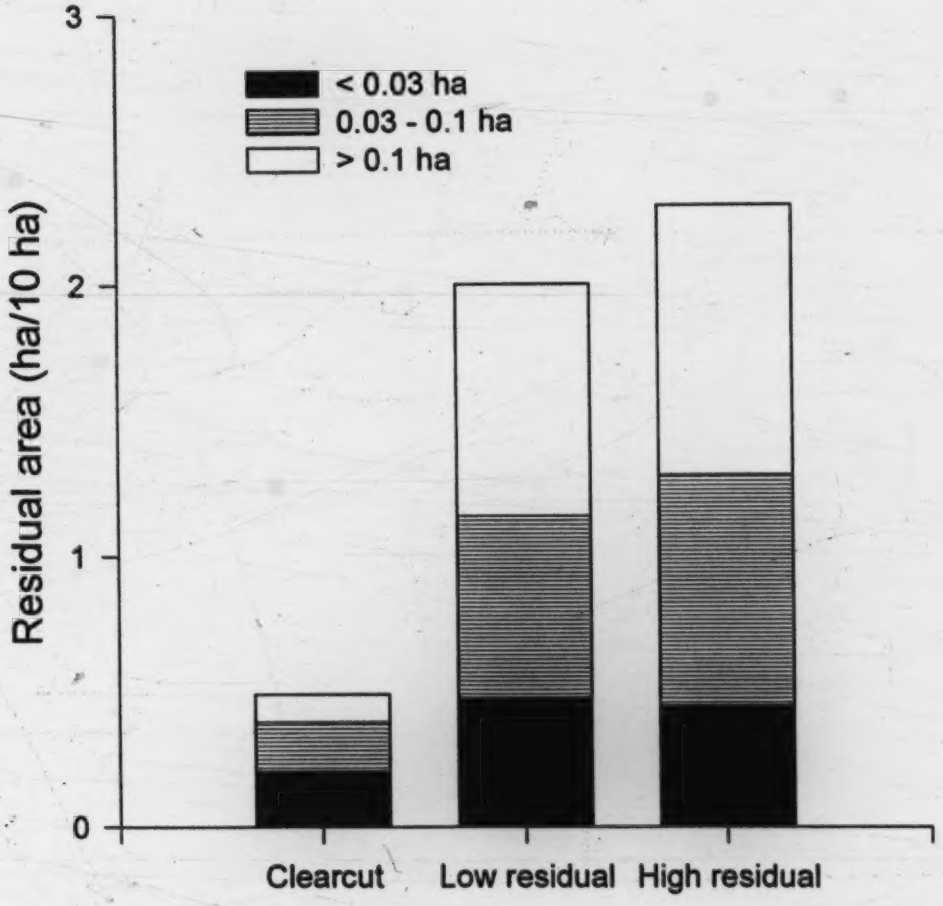

Figure 2-3: Area of residual vegetation per 10 ha total cutblock size. Patch sizes correspond to individual trees of groups of a few trees (< 0.03 ha), small patches with disturbed understorey (0.03 - 01 ha), and large patches with intact understorey (> 0.1 ha). There is no significant difference in the proportions of the 3 patch size classes between treatments.

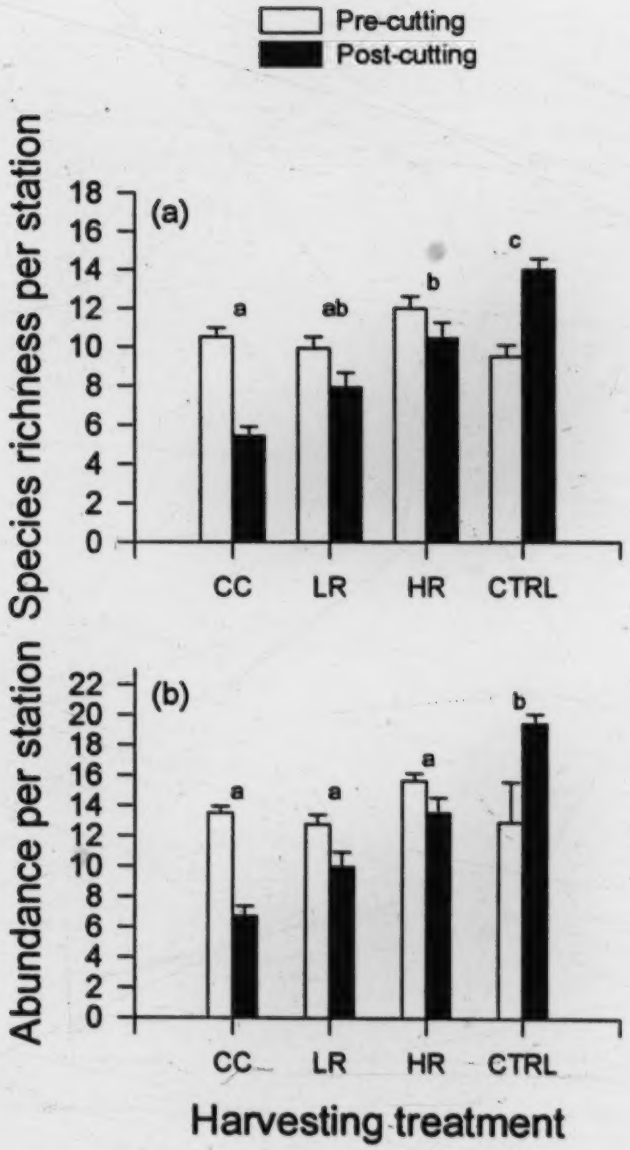

Figure 2-4: Species richness (a) and bird abundance (b) per census station across treatments before and after logging; standard errors are indicated. Richness and abundance both increased significantly in the controls between years but decreased significantly in all harvesting treatments when contrasted with control sites. Changes in richness and abundance between years were not significantly different for treatments with the same letter. (CC, clearcut; LR, low residual; HR, high residual; CTRL, control).

clearcut and low residual treatments (one-way ANOVA, Scheffé post-hoc comparisons, $\alpha = 0.05$). The percentage decrease in bird abundance was strongly correlated with the percentage of vegetation cover retained on each cutblock after removing the road allowance ($r^2 = 0.64$). The slope of this relationship was 1.39, indicating that small increases in vegetation cover can have a relatively larger effect on bird density.

Although species richness dropped on a per station basis on harvested sites, the total species pool only declined in clearcuts (Table 2-2). However, turnover was inversely related to the amount of vegetation retained, as evidenced by lower values of Jaccard ($F = 9.63$, $p = 0.005$) and Phi-square ($F = 11.68$, $p = 0.02$) similarity indices in sites with less residual vegetation, indicating species replacement (Table 2-2). The clearcut sites lost 13 species and gained 6 in the post-cutting year. The partial-cuts and the controls showed fairly similar patterns: the partial-cuts combined lost 3 species and gained 6, the controls lost 2 species and gained 8. Species gained in the harvested sites were mostly birds of open areas or shrubby habitats, and included Dark-eyed Junco, Alder Flycatcher, Lincoln's Sparrow, Western Wood-Pewee, and House Wren (for scientific names see Appendix 2); the latter two were new species to the entire study area. Species gained in the controls were mostly forest dwelling species: Hermit Thrush, Ruby-crowned Kinglet, Gray Jay, Solitary Vireo, Black and White Warbler, Tennessee Warbler, Ovenbird, and Dark-eyed Junco.

2.3.3 Response to harvest by nesting and foraging guilds

Grouping species by foraging and nesting guilds pinpointed the changes in bird abundance (Fig. 2-4). There was no difference in the response of ground foraging guilds to the different harvesting treatments; abundance increased slightly between years in all treatments. The abundance of ground nesting birds increased in low residual and control sites relative to slight decreases in clearcut and high residual sites. Significant declines were observed after harvesting in the tree and shrub nesting guild ($F = 17.33$, $p = 0.001$) and the foliage gleaning foraging guild ($F = 8.20$, $p = 0.01$) and the magnitude of the change was similar among harvested treatments. Cavity nesting birds showed a trend towards a negative response to harvesting, but small sample sizes hampered the analysis

Table 2-2: Species richness in each cutblock size class (x̄ = 12.2, 22.8, 29.4 ha respectively) and harvesting treatment, before (1994) and after (1995) harvest. Jaccard index, x̄ (SE), measures similarity of species composition between years, Phi Square index, x̄ (SE), incorporates species relative abundances; both are expressed as ecological similarity. Treatments with the same letter are not significantly different (one-way ANOVA, $\alpha = 0.05$).

		Block Size					
		Small	Medium	Large	Total	Jaccard	Phi Square
Clearcut	1994	18	16	18	24	0.253 (0.047)[a]	0.347 (0.017)[a]
	1995	5	11	12	17		
Low residual	1994	14	18	17	24	0.370 (0.015)[ab]	0.320 (0.023)[a]
	1995	12	15	17	23		
High residual	1994	14	16	24	26	0.544 (0.074)[b]	0.453 (0.036)[ab]
	1995	14	12	18	24		
Control	1994	13	17	20	22	0.571 (0.036)[b]	0.542 (0.032)[b]
	1995	20	16	23	28		

($F = 0.98$, $p = 0.45$). Aerial foraging birds decreased in abundance after logging on harvested sites, but the trend was not statistically significant ($F = 2.30$, $p = 0.164$). After logging, there was a significant trend of decreasing bird abundance from controls to clearcuts in the foliage gleaning ($F = 16.73$, $p = 0.001$), aerial gleaning ($F = 4.95$, $p = 0.037$), ground nesting ($F = 6.20$, $p = 0.022$), and tree/shrub nesting ($F = 42.76$, $p < 0.001$) guilds (Table 2-3). Species richness also showed a trend towards lower values on clearcut sites.

2.3.4 Response to harvest by individual species

Overall, on clearcuts 41% (12/29) of species decreased in abundance between years, 31% (10/32) decreased in the partial-cuts, but only 3% (1/32) decreased in the controls. In contrast, the figures for species showing increases between years were 3% (1/29) in clearcuts, 9% (3/32) in partial-cuts, and 19% (6/32) in the controls. Of species that were not observed on clearcuts after harvest, the decrease in abundance was significant for 8 species: Red-breasted Nuthatch, Winter Wren, Swainson's Thrush, Black-throated Green Warbler, Canada Warbler, American Redstart, Rose-breasted Grosbeak,

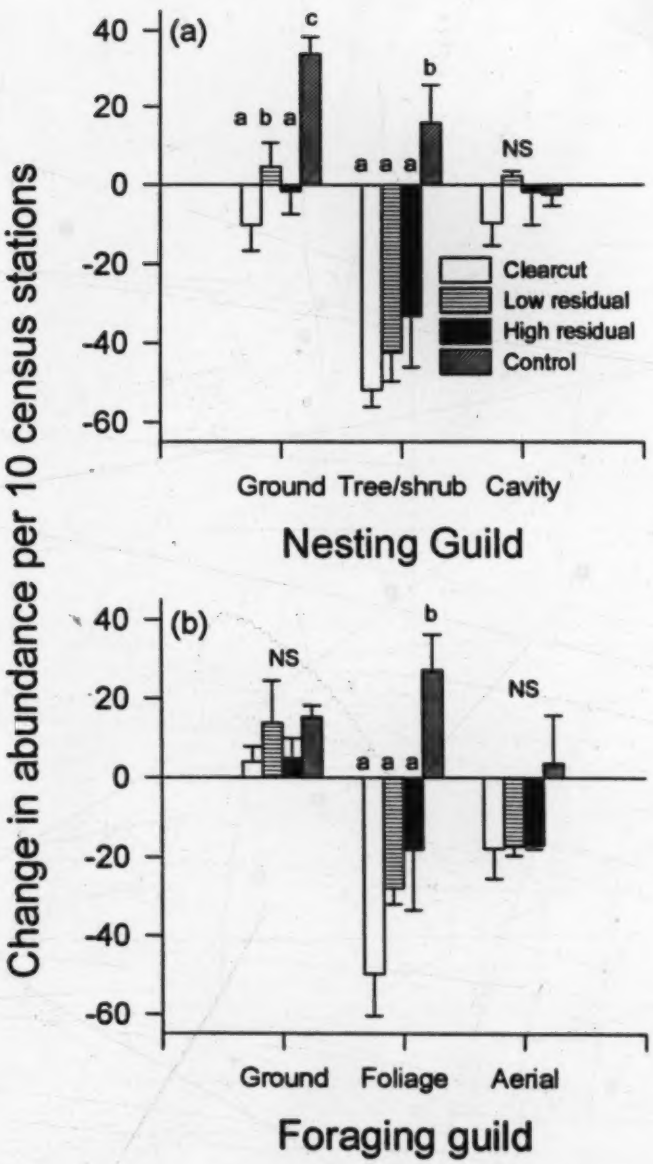

Figure 2-5: Change in bird abundance within nesting (a) and foraging (b) guilds after harvesting. Values are expressed as the mean (standard error) number of presumed pairs per 10 census stations lost/gained for each harvesting treatment. Bars within the same guild with the same letter are not significantly different.

Table 2-3: Bird abundance (x̄ (SE) per 10 census stations) and species richness (total number of species) within each foraging and nesting guild for each harvesting treatment. Guilds exhibiting a significant trend in abundance across treatments are shown in **bold**.

	Clearcut		Low residual		High residual		Control	
	Abundance (SE)	Species Richness	Abundance (SE)	Species Richness	Abundance (SE)	Species Richness	Abundance (SE)	Species Richness
Foraging								
Ground	45.2 (4.0)	7	48.3 (4.6)	8	42.8 (4.0)	8	45.8 (3.7)	8
Foliage	13.4 (7.0)	6	29.6 (5.4)	5	47.8 (13.8)	9	83.0 (1.5)	11
Aerial	3.7 (1.9)	3	13.1 (1.7)	7	23.9 (5.9)	4	36.8 (9.9)	5
Nesting								
Ground	47.7 (7.4)	6	58.4 (0.9)	7	55.7 (7.4)	8	78.3 (3.9)	9
Tree/shrub	11.8 (2.7)	8	24.7 (2.7)	11	49.9 (12.7)	11	85.0 (7.6)	15
Cavity	3.1 (1.6)	3	10.8 (4.5)	4	10.1 (5.0)	4	11.4 (5.6)	4

and Western Tanager. All of these species except Western Tanager, however, were present in the partial-cuts, although at lower abundances than in the controls.

Twenty-two out of 36 species (61%) differed between years and/or harvesting treatment (Table 2-4), although small sample sizes hampered analyses for some species. The abundances of 18 species changed significantly after logging (Table 2-4). All but four of these had lower abundances after logging; Lincoln's Sparrow and House Wren were most abundant in the clearcuts, Chipping Sparrow was most abundant in the partial-cuts. Tennessee Warbler increased greatly in abundance over the entire study area, but increases on harvested sites were less than in the controls. Several species were present in all sites, notably the White-throated Sparrow which was the most abundant species in all treatments before and after logging.

2.4 Discussion

2.4.1 Community-level response

The pattern of bird species richness and abundance after logging supported our main prediction: bird communities in harvested sites with less residual vegetation had greater species turnover and lower bird abundances. This was seen despite an overall increase in abundance in 1995 on control sites. Partially-cut sites were intermediate to clearcuts and controls by all measures. The increase in species richness and abundance in undisturbed forest in 1995 may have been due to a crowding effect (Whitcomb *et al.* 1981) whereby returning migrants of some species were forced into a reduced forest area following logging. I feel this explanation is unlikely because the harvested area was very small compared to the extensive forest present on the larger landscape. The increases were also noted in a study conducted within 10 km of this one (Schmiegelow *et al.* In press) suggesting a general increase in abundance of many species throughout the area. It should be noted that the repeated measures analysis implicitly assumes that the increases in richness and abundance in the controls were not a result of logging and would have occurred irrespective of logging activity.

Some studies have found little influence of partial-cut harvesting on bird communities (Scott and Gottfried 1983, Medin and Booth 1989, Ziehmer 1993). Medin

Table 2-4: Species abundances before (1994) and after (1995) logging in three harvesting treatments (CC: structured clearcut, PC: partial-cut, CTRL: uncut). Foraging and nesting guilds as discussed in text are given for each species. Abundances are expressed as number of presumed pairs per 10 census stations (approximately 50 ha) per treatment, estimated from point counts (n = 14 stations for CC and CTRL, n = 26 for PC). Abundances of zero are omitted. Significant differences in abundances between years are indicated with an asterisk under 'Post-cutting' (Wilcoxon matched-pairs signed-rank test). Associated probabilities are given for species showing a significant difference in abundance between treatments post-cutting (Kruskal-Wallis ANOVA). Species identified as selecting for older stands (Schieck and Nietfeld 1995) are given in bold type.

Species	Foraging Guild[a]	Nesting Guild[b]	Pre-cutting			Post-cutting			Treatment Variation
			CC	PC	CTRL	CC	PC	CTRL	
Yellow-Bellied Sapsucker	B	C	2.5	1.2	1.79	0.36*	1.53	0.71	
Western Wood-Pewee	A	ST				2.14	0.38		
Least Flycatcher	A	ST	0.71	5.2	5		2.69	4.29	
Alder Flycatcher	A	ST			0.71	0.71	1.92*	0.71	
Gray Jay	G	ST	1.43	0.53		1.79	1.25	2.50*	p = 0.019
Black-Capped Chickadee	FG	C		0.4		0.35	2.5		
Brown Creeper	B	C	1.43	4	5		0.38*	4.29	
Red-Breasted Nuthatch	B	C	3.57	2.8	2.14	*	0.38	2.86	
House Wren	G	C				2.86			p = 0.013
Winter Wren	G	C	3.57	2.4	5	*	3.85	4.29	
Golden-Crowned Kinglet	FG	ST	0.71		0.71				

Table 2-4 cont'd

Species	Foraging Guild[a]	Nesting Guild[b]	Pre-cutting			Post-cutting			Treatment Variation
			CC	PC	CTRL	CC	PC	CTRL	
Ruby-Crowned Kinglet	FG	ST		1.2				2.14	P = 0.016
Swainson's Thrush	FG	ST	6.78	9	5	*	1.53*	5.71	p = 0.011
Hermit Thrush	G	G					1.15	3.57	
American Robin	G	ST	1.78	0.4	0.71	2.5	2.31	0.71	
Solitary Vireo	FG	ST	1.43	0.4				0.71	
Red-Eyed Vireo	A	ST	13.57	13.6	9.29	1.43*	8.46*	12.86*	p < 0.001
Warbling Vireo	FG	ST	1.43	4.4	3.57	2.14	1.92	1.43*	
Philadelphia Vireo	A	ST					0.38		
Tennessee Warbler	FG	G	4.29	1.6		5	6.15*	11.43*	p < 0.001
Black-and-White Warbler	B	G						1.43	
Magnolia Warbler	A	ST		1.2			0.77		
Yellow-Rumped Warbler	FG	ST	10.71	10.4	9.29	0.71*	3.85*	10.71	p = 0.006
Black-Thr. Green Warbler	FG	ST	10	11.2	7.14	*	1.15*	12.86	p = 0.001
Yellow Warbler	FG	ST		2.8	7.14	1.43	2.69	6.43	

Table 2-4 cont'd

Species	Foraging Guild[a]	Nesting Guild[b]	Pre-cutting			Post-cutting			Treatment Variation
			CC	PC	CTRL	CC	PC	CTRL	
Mourning Warbler	FG	G	15.71	15.6	16.43	6.43*	11.54	16.43	P = 0.006
Canada Warbler	A	G	4.29	5.2	3.57	*	0.38*	3.57	
Ovenbird	G	G	3.57	4.4			0.76*	4.29*	p < 0.001
American Redstart	A	ST	5.71	10	17.14	*	1.92*	11.43	
Rose-Breasted Grosbeak	FG	ST	5	1.6	2.14	*	1.15	5.71*	p < 0.001
Chipping Sparrow	G	G	5	3.2	0.71	7.14	11.73*	3.57*	P = 0.044
Dark-Eyed Junco	G	G		0.4		2.14	0.57	0.71	
White-Throated Sparrow	G	G	22.86	23.2	21.07	20.71	19.42	20.71	
Lincoln's Sparrow	G	G	2.14		2.14	8.57*	3.46*		p = 0.004
Western Tanager	FG	ST	5.71	3.2	2.14	*	*	2.86	P = 0.026
Purple Finch	G	ST					0.38		

[a] G, ground forager; FG, foliage gleaner; A, aerial or hover gleaner; B, bark gleaner.
[b] G, ground nester; ST, shrub or tree nester; C, cavity nester.

and Booth (1989), and Scott and Gottfried (1983) conducted their work in conifer dominated forests with very different bird communities from ours, whereas Ziehmer's (1993) study was conducted in hardwood forests in Missouri and involved many of the same bird species found in my study area. However, the vegetation retention levels examined were much higher than in my study, and harvesting methods were single-tree or small group selection methods. Freedman *et al.* (1981) found, similar to this study, that bird abundances were slightly reduced on partially-cut treatments, but that community composition was altered as well.

In my study, the logging operators decided what was to be cut or retained as they worked, and patch sizes varied greatly and residual material was not completely uniformly distributed over the blocks. Crawford *et al.* (1981) concluded that canopy cover and the tall and low shrub layers were the most important components of vegetation for maintaining bird communities. In my study, approximately one third of retained vegetation was as individual trees, or clumps of stems too small to have any intact understorey and thus may have had little functional importance to birds.

2.4.2 Response by guilds and individual species

The response of birds in different foraging and nesting guilds to the harvested treatments were consistent with our predictions. Ground nesting/foraging species were affected less by harvesting treatment than species found in tree or shrub layers. The ground guilds thus may be less dependent on the tree or shrub layers, at least on the short term. Ground guilds include a similar number of Neotropical migrants as other guilds, so migratory status does not confound this result. Even ground guilds were affected by logging, however, because the relative abundances of constituent species shifted after logging. Those species more characteristic of open habitats, such as Lincoln's Sparrow, made up a larger proportion of the total abundance after logging. The White-throated Sparrow appears to be a true habitat generalist because it was the most abundant species in all sites. The dramatic increase of Tennessee Warblers in 1995 was seen in other studies in the area (Chapter 3, Schmiegelow *et al.* In press), but the cause of the increase is not clear. Although Brown-headed Cowbirds (*Molothrus ater*) were very rare in our

study area, the region is still largely covered with intact forest, such that the logging done for this study essentially created edge within an otherwise highly forested landscape. Rates of Cowbird parasitism have been found to be low in relatively undisturbed landscapes (Robinson *et al.* 1995), but as logging proceeds, Cowbird populations might increase in response to the creation of forest openings.

Of the 22 species showing a significant effect of logging in this study, 19 declined in abundance, and 11 of these were not recorded on clearcut sites, whereas only one, Western Tanager, was also excluded from partial-cuts. Eleven of these 22 species have been identified as selecting moderately to strongly for older forest stands (Schieck *et al.* 1995, Table 4). All of these except Winter Wren and Chipping Sparrow require trees or shrubs for foraging or nesting (Ehrlich *et al.* 1988) and all except Western Tanager were maintained at higher abundances on partial-cuts than clearcuts. However, abundances were lower than in uncut sites. These are species which are at most risk from forest cutting practices which preferentially target the clearcutting of old stands which is the current practice in Alberta (Anonymous 1992).

2.4.3 Scope and limitations

Although this study's results are strengthened by a before-and-after-treatment design, data are only presented for one year post-logging before any regrowth of aspen or shrubs had occurred. Suitable habitat for birds of second-growth habitats will likely be produced as the stands regenerate (Westworth and Telfer 1993) and songbirds characteristic of older stands might return to pre-cut levels more rapidly in partial-cuts than clearcuts. Simply noting declines immediately after logging might give an unrealistically negative picture of the effects of partial-cutting. Freedman *et al.* (1981) found that on 3-5 year old selectively-cut plots bird densities were roughly equal to those on control plots, and that community composition was intermediate between clearcut and control plots. A longer-term picture through periodic monitoring of our study blocks would allow a fairer assessment.

It is also possible that results were slightly confounded by the fact that the controls appeared to be slightly older despite their being chosen in similar stands based on

vegetation maps. Bird communities were not detectably different overall before logging, however, so we have no reason to suspect any significant confounding. Some species abundances were somewhat skewed towards certain treatments (*e.g.* Yellow Warbler, Red-eyed Vireo, see Table 2-4), so conclusions that can be made from our data are limited for those species.

A critical consideration in assessing the benefits of any harvesting prescription regards the reproductive potential of birds inhabiting such areas, because the longer-term persistence of birds in partial-cuts depends entirely on the viability of such populations. An original intent of this study was to produce relative indices of reproduction in the partial-cuts and controls to compare the reproductive potential of birds inhabiting the different treatments (after Vickery *et al.* 1992), but logistical problems prevented the collection of these data in a meaningful, quantitative manner. The reproductive success of birds in harvested sites may be lower than in undisturbed forest because the abundance of canopy-dwelling insects might be reduced in proportion to the canopy cover removed, and food abundance has been shown to influence territory size (Cody and Cody 1972, Smith and Shugart 1987). For canopy-foraging species, this might necessitate the maintenance of a larger territory in the disturbed areas with less energy being devoted to reproduction. One study of bird response to selective harvesting which attempted to measure a parameter relating to reproduction found, with a very small sample size, that male Red-eyed Vireos inhabiting selectively logged plots failed to find a mate (Ziehmer 1993).

2.5 Considerations for Forest Management

Clearcut logging associated with industrial forestry may pose a significant threat to some wildlife species and natural communities (Cumming *et al.* 1994). One often cited alternative to clearcutting is the use of partial-cut or selective harvesting techniques to maintain some wildlife habitat value on harvested sites. The type of partial-cutting studied here differs from other selective harvest techniques, such as shelterwood cutting, in that no second pass harvest is planned. Residual vegetation will be allowed to age naturally until the cut area reaches rotation age (approximately 80 years). This may help produce characteristics of older stands such as snags, down logs, and canopy gaps, in a stand

fundamentally too young to contain such features (Schieck *et al.* 1995). Periodic monitoring of these study blocks in the future would be necessary to evaluate whether songbirds characteristic of older stands return to pre-cut levels more rapidly in partial-cuts than clearcuts. Also, the intent of this study was to examine a method of partial-cutting which would be logistically feasible for use with the mechanization typically used for clearcut logging. This constrained vegetation retention to much lower levels. Retention approaching 50% is probably the upper limit for this type of logging.

The current trend in forest management in Alberta is to shift from sustained-yield to ecosystem-based management. One of the main thrusts of this approach is to attempt to maintain ecological processes in a managed landscape (Grumbine 1994). In the boreal mixed-wood forest the principal natural disturbance agent is fire, and a goal of forest harvesting under an ecosystem management paradigm is therefore to approximate characteristics of burned areas in cutblocks. Little work has yet been done on the distribution of residual vegetation in burned areas, but Eberhardt and Woodard (1987) found that fires of 20-40 ha contained no residual islands greater than 1 ha and that residual material varied greatly among burned areas. Small fires typically contain above-ground structure as dead tree stems and very small patches of trees. The value of partial-cuts to an ecosystem management approach would lie in expanding the range of variation of residual material present on cutover areas over a managed landscape.

Partial-cutting may be of use in a system of forest management that is based primarily on a two-pass clearcutting harvesting schedule. Retained vegetation structure appears to reduce the negative impacts of clearcutting on songbirds, by providing increased possibilities for breeding or foraging, and may also help maintain bird movement in a fragmented landscape. This study only considered one year post-harvest before any regeneration of aspen saplings or shrubs. Benefits could become more pronounced as the stands regenerate. Partially cut blocks may also reduce negative impacts of forest harvesting on uncut leave areas. Lower contrast in vegetation structure between cut and uncut areas might increase the effective area of leave areas by providing additional foraging opportunities not afforded by clearcuts and may reduce the potential for negative

effects associated with sharper edges. Additionally, increased vegetation structure may reduce the degree to which harvested areas act as barriers to the movement of birds between forest patches (Machtans *et al.* In press). Such movement may be critical to the persistence of species in a fragmented landscape (Harrison 1994). However, given demand for a constant fibre supply, a larger amount of forest would need to be disturbed under a widespread partial-cutting regime, so this might be a poor option on a large scale.

Finally, it must be remembered that specific conservation goals, human values, and economic considerations must all be incorporated into any large-scale management plan (Grumbine 1994). Partial-cutting may, in certain circumstances, prove to be a useful tool in site-specific, local-scale management for particular wildlife habitat attributes or aesthetic values. However, because the benefits to songbirds of partial-cuts over clearcuts appear slight, this form of harvesting is not likely to achieve a conservation goal of maintaining bird communities that are similar to those found in undisturbed forest.

2.6 Acknowledgements

I gratefully acknowledge the cooperation of Alberta-Pacific Forest Industries Inc., especially Daryl Hebert and Shawn Wasel for suggesting this study, and Kari Stuart-Smith and Helmut Roeben for their logistical support. The efforts of Redwood Logging Ltd. and Dave Usher during the harvesting operations were greatly appreciated. Thanks to Josette Landry of Pearson Timberline Forestry Consultants for assistance with the air photo interpretation, and John Brzustowski for help with the GIS. Craig Machtans, Ian Adams, Kari Stuart-Smith, Jim Schieck, Kathy Martin, Wendy Easton, John Faaborg and an anonymous reviewer provided valuable comments on earlier drafts of this chapter. The study was supported financially by Alberta-Pacific Forest Industries Inc., a Canadian Circumpolar Institute BAR grant, an NSERC Industrial postgraduate scholarship to MRN, and an NSERC operating grant to SJH.

2.7 Literature Cited

Anonymous. 1992. Timber harvesting planning and operation ground rules. Alberta Energy/Forestry, Lands and Wildlife Publ. No. 67. Edmonton, AB. 75 pp.

Blake, J.G., Hanowski, J.M., Niemi, G.J., and Collins, P.T. 1994. Annual variation in bird populations of mixed conifer-northern hardwood forests. Condor **96**: 381-399.

Blondel, H., Ferry, C., and Frochot, B. 1981. Point counts with unlimited distance. Studies in Avian Biology **6**: 414-420.

Cody, M.L., and Cody, C.J.B. 1972. Territory size, food density and clutch size in island wren populations. Condor **74**: 473-477.

Crawford, H.S., Hooper, R.G., and Titterington, R.W. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. J. Wildl. Manage. **45**: 680-692.

Cumming, S.G., Burton, P.J., Prahacs, S., and Garland, M.R. 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: A simulation study. For. Ecol. Manage. **68**:281-302.

Devall, B., editor. 1993. Clearcut: the tragedy of industrial forestry. Sierra Club Books/Earth Island Press: San Francisco, CA. 291 pp.

Eberhart, K.E., and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. **17**:1207-1212.

Ehrlich, P.R., Dobkin, D.S., and Wheye, D. 1988. The birder's handbook: A field guide to the natural history of North American birds. Simon and Schuster Inc.: Toronto, ON. 785 pp.

Franzreb, K.E., and Ohmart, R.D. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor **80**: 431-441.

Freedman, B., Beauchamp, C., McLaren, I.A., and Tingley, S.I. 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. Can. Field-Nat. **95**: 307-311.

Grumbine, R.E. 1994. What is ecosystem managment? Conserv. Biol. **8**:27-38.

Harrison, S. 1994. Metapopulations and conservation. pp. 111-128 in: P.J. Edwards, R.M. May, and N.R. Webb, eds. *Large scale ecology and conservation biology*. Blackwell Scientific Pubs.: Oxford, UK.

Jackson, D.A., Somers, K.M., and Harvey, H.H. 1989. Similarity coefficients: Measures of co-occurrence and association or simply measures of occurrence? Am. Nat.

133: 436-453.

Kent, M., and Coker, P.. 1992. Vegetation description and analysis: A practical approach. CRC Press: Boca Raton, FL. 363 pp.

Ludwig, J.A., and Reynolds, J.F. 1988. Statistical ecology: A primer on methods and computing. J. Wiley & Sons: Toronto, ON. 337 pp.

Machtans, C.S., Villard, M.-A., and Hannon, S.J. In press. Use of riparian buffer strips as movement corridors by forest birds. Conserv. Biol.

Martin, T.E. 1992. Breeding Biology Research Database (BBIRD) program: General overview and standardized protocols. U.S. Dept. of the Interior, Fish and Wildlife Service, Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas, Fayetteville, AR.

Medin, D.E., and Booth, G.D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. Res. Pap. INT-408. USDA Forest Service Intermountain Research Station, Ogden, UT. 11 pp.

Mladenoff, D.J., White, M.A., Crow, T.R., and Pastor, J. 1994. Applying principles of landscape design and management to integrate old-growth forest enhancement and commodity use. Conserv. Biol. **8**: 752-762.

Morton, E.S. 1992. What do we know about the future of migrant landbirds? pp. 579-589 in: J.M. Hagan and D.W. Johnson, eds. *Ecology and management of Neotropical migrant landbirds*. Smithsonian Inst. Press: Washington D.C.

Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., and DeSante, D.F. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. 41 pp.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution **43**: 223-225.

Robbins, C.S., Sauer, J.R., Greenberg, R.S., and Droege, S. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. USA **86**: 7658-7662.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R., and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987-1990.

Scheiner, S.M. 1993. MANOVA: Multiple response variables and multispecies

interactions. pp. 94-112 in: S.M. Scheiner and J. Gurevitch, eds. *Design and analysis of ecological experiments*. Chapman and Hall: New York, NY.

Schieck, J., Nietfeld, M., and Stelfox, J.B. 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. Can. J. Zool. **73**:1417-1431.

Schmiegelow, F.K.A., Machtans, C.S., and Hannon, S.J. In press. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology.

Scott, V.E., and Gottfried, G.J. 1983. Bird response to timber harvest in a mixed conifer forest in Arizona. Res. Pap. RM-245. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 8 pp.

Smith, T.M., and Shugart, H.H. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology **68**: 695-704.

Thompson, F.R. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conserv. Biol. **7**: 325-333.

Thompson, F.R, Dijak, W.D., Kulowiec, T.G., and Hamilton, D.A. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. J. Wildl. Manage. **56**: 23-30.

Thompson, F.R, Probst, J.R., and Raphael, M.G. 1993. Silvicultural options for Neotropical migratory birds. pp. 353-362 in: D.M. Finch and P.W. Stangel, eds. *Status and management of Neotropical migratory birds*. Gen. Tech. Rep. RM-229. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Vickery, P.D., Hunter, M.L., and Wells, J.V. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. Auk **109**: 697-705.

Welsh, D.A. 1987. The influence of forest harvesting on mixed coniferous-deciduous boreal bird communities in Ontario, Canada. Acta Oecologia **8**: 247-252.

Westworth, D.A., and Telfer, E.S. 1993. Summer and winter bird populations associated with five age classes of aspen in Alberta. Can. J. For. Res. **23**: 1830-1836.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimliewcz, M.K., and

Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. pp. 125-205 in: R.L. Burgess and D.M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag: New York, NY.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**: 1211-1214.

Ziehmer, R.L. 1993. Effects of uneven-aged timber management on forest bird communities. M.Sc. Thesis, University of Missouri, Columbia, MO. 62 pp.

CHAPTER 3

The importance of different spatial perspectives in assessing songbird response to landscape fragmentation.

3.1 Introduction

The dramatic rate at which humans are fragmenting previously contiguous landscapes has been a concern of conservationists and the focus of intensive scientific research for the better part of two decades (*e.g.* Forman *et al.* 1976, Wilcove *et al.* 1986). Changes such as a reduction in original habitat area, isolation of remaining habitat patches, and an increase in edge habitat relative to interior habitat have all been implicated as having negative effects on some wildlife populations (Saunders *et al.* 1991). Declines in several species of birds have been partially attributed to the fragmentation of the breeding habitat (*e.g.* Whitcomb *et al.* 1981, Böhning-Gaese *et al.* 1993), and neotropical migrant birds appear to be particularly sensitive (Robbins *et al.* 1989, Morton 1992). The boreal forest of northern Alberta provides breeding habitat for 48 of these neotropical migratory species (Smith 1993), and is under increasingly heavy pressure from the forest industry.

Our perception of the impacts of fragmentation has been heavily based on the Theory of Island Biogeography (MacArthur and Wilson 1967). This theory has dominated not only our thinking about which variables to measure (Wiens 1994) but has also kept us focussed on the somewhat simplistic concept of the 'patch' in the design of our experiments. Studies have generally focussed on individual patches of a particular habitat type at some arbitrary spatial scale. However, there is emerging evidence that scale is an important factor in ecological research (Addicott *et al.* 1987, Turner 1989, Wiens 1989*a*); in fact, scaling has been referred to as the fundamental conceptual problem in ecology (Levin 1992).

It is not immediately clear which spatial scale is most appropriate to studies of forest fragmentation. It has been implicitly assumed that fragmentation occurs in a coarse-grained manner (Lord and Norton 1990, Rolstad 1991); that is, that habitat fragments are larger than a single territory and that the resulting patchiness is at a scale which species respond to (Kotliar and Wiens 1990). Different spatial perspectives may still affect our

interpretation of species' responses, however. For instance, small scale extinctions may appear only as a spatial redistribution at a broader scale (Villard *et al.* 1992). More generally, rarer species may follow a different scaling function in their habitat use than more common species (Wiens 1989*a*). Species dependent on sparse or clumped resources may function at larger scales than those species using abundant or uniformly distributed resources (O'Neill *et al.* 1988).

Although researchers have tended to view habitat fragments in isolation from the surrounding landscape, habitat fragments are not embedded in a totally inhospitable matrix (Wiens 1994). A consideration of only one stand type may be misleading because many bird species have wider habitat usage patterns than one particular stand type, and some individuals may include more than one patch type within their territory (Haila *et al.* 1989). In a process similar to what Dunning *et al.* (1992) have termed landscape supplementation, species may shift their habitat selection to other stand types following fragmentation of their preferred habitat. The boreal forest, where this study was conducted, is a landscape which is naturally patchy and within which particular stand types are spatially distinct even without human intervention (Hansson 1992). Studies which incorporate only one focal habitat type miss a significant component of the boreal bird community. Only with a broad, landscape view can we hope to detect and properly interpret all changes in bird communities following forest fragmentation.

Scale is a potentially important factor not considered previously in fragmentation studies but which could affect our interpretations of the effects of forest fragmentation, and therefore hinder conservation efforts designed to mitigate the problem. This study addresses the issue by taking a multi-scale approach (Maurer 1985, O'Neill *et al.* 1986, Schneider 1994). Specifically, the following questions were posed:

1. Does fragmentation by clearcut logging affect songbird communities in remaining patches of forest? I approach this first question at a 'typical' spatial scale: several aspen forest patches over a landscape of arbitrary size.
2. Are effects of fragmentation still evident when the whole landscape is included

in the analysis?

3. Are fragmentation effects consistent across spatial scales? Here I return the focus to aspen forest patches, but the view the system of Question 1 from a second, larger, spatial scale.

4. Is there a biologically relevant scale to work at?

The forest of north-central Alberta provided the setting as a typical boreal landscape which is under heavy pressure from industrial logging activity. Community parameters of species richness, bird abundance, and turnover, as well as individual species data were analyzed to begin understanding scale-dependence in the response of songbirds to widespread landscape fragmentation.

3.2 Methods

3.2.1 Study Site

The study area was located in the boreal mixed-wood region (Rowe 1972) near Calling Lake, Alberta (55°15'N 113°19'W), approximately 250 km north of Edmonton. Forests in the area are pyrogenic, and primary forest succession in this region is dominated by trembling aspen (*Populus tremuloides*) with lesser amounts of balsam poplar (*P. balsamifera*). The principal coniferous tree species are white spruce (*Picea glauca*) and black spruce (*P. mariana*) and mixed stands of aspen and spruce are common. A natural mosaic of deciduous, coniferous and mixed stands across the landscape is maintained by frequent disturbances such as fire and by drainage and topography. Aspen stands, the primary focus in this study, originated after fire between 1900 and 1920; no logging had previously occurred in the area, but forests had been disturbed by the clearing of seismic exploration lines (roughly 6 m wide) and natural-gas well construction.

I delineated a treatment and a reference landscape, each roughly 70 km^2. The landscapes were matched for their proportions of different habitat types using Alberta Phase 3 Forest Inventory maps. The first pass of clearcut harvesting of aspen took place on the treatment area during the winter of 1993-94. Harvesting followed a roughly checkerboard pattern, with cut patches averaging approximately 30 ha (range 3 ha to 60 ha) and equivalent sized fragments (leave-areas) left for a second-pass harvest in

approximately 10 years. Harvesting targeted aspen stands exclusively and all coniferous and mixed stands (>20% conifer approximately) were left intact. The reference (unlogged) area was located adjacent to the treatment area and was undisturbed excepting the seismic lines and one winter-use road. A buffer of 400 m was left between sampling areas for treatment and reference to minimize the likelihood of direct fragmentation effects influencing the reference area (although note that Cotterill [1996] found no evidence of edge effects on nest predation rates in the area).

3.2.2 Data Collection and Preliminary Analyses

An understanding of the basic elements of field sampling and some of the initial manipulations of the data sets makes comprehension of the rather complex combination of study design and data analysis procedures easier. Readers familiar with point-count censusing of birds and plot-based vegetation sampling may wish to skip to § *3.2.3 Study Design and Data Analysis*.

3.2.2.1 Bird Census

The basic sampling units were census stations arranged within leave-areas and matching reference areas. Songbird communities were surveyed using a fixed-radius point-count technique following standards recommended by Ralph *et al.* (1993). Birds were recorded within radii of 50 m and 100 m. Forest patches were sampled at an intensity of approximately one census station per 5 ha, and stations were located 200 m apart to minimize double-counting of birds at adjacent stations. We surveyed birds at the peak of the breeding season each year (late May to early July), from sunrise until 10:00 am. Trained observers were rotated among sites. Each station was visited 3 times in 1994 and 4 times in 1995 for 5 minutes per visit; only 3 census rounds of corresponding dates were used for between year comparisons. One or more registrations of a singing male over the 3-4 rounds was required to record the species as present in a site; simultaneous registrations of singing males were required to accept more than one pair at a given station. Singing males, observed pairs, and nests were scored as 1.0, silent or calling birds were scored as 0.5. Abundances at a given station was calculated as the maximum number of presumed pairs recorded for each species on a given visit to a station (Blondel

et al. 1981, Blake *et al.* 1994). Bird densities were not calculated because of the requirement of accurate distance estimates for each bird detection (Blake *et al.* 1994).

The exact locations of each census station from aspen leave-areas and reference sites were measured with a *Geo*Explorer® geographic positioning system. All files were differentially corrected using PFINDER software (Trimble Navigation Ltd. 1992) to obtain 2-5 m accuracy of positions.

3.2.2.2 Vegetation Data Collection and Preliminary Analyses

Vegetation data were collected at all sites based on a modified version of the protocol of Martin (1992). Three 0.04 ha circular plots were surveyed at each point count station, with plots located 30 m from the station at angles of 0°, 120° and 240°. The following data were collected: percent ground cover was estimated for 7 vegetation classes (all green, forb, low shrub [<1 m], grass, moss/fern, coarse woody debris [downed woody material ≥ 5 cm diameter], leaf litter) in four 1 m^2 quadrats per plot; number of stems for each shrub species was determined in the same 4 quadrats; number of small trees (<2.5 cm and 2.5 - 8.0 cm diameter at breast height [dbh]) by species in 0.008 ha sub-plots; number of trees by species in 4 dbh classes (8-15, 15-23, 23-38, >38 cm) in the total plot; number of snags 8-12 cm dbh in the total plot; species, height and dbh of snags > 12 cm dbh in the total plot; heights of the canopy, subcanopy and tall shrub layers (measured with a clinometer); and canopy cover (measured with a spherical densiometer).

As collected, the vegetation data set contained over 100 variables. I reduced the number of variables to a more manageable 24 which captured the range of variation more efficiently. All variables were standardized to a mean of 0 and standard deviation of 1 prior to all analyses. Vegetation data did not conform to the assumptions necessary for a multivariate ANOVA to test whether the logged and reference landscapes were in fact similar in terms of local scale vegetation structure. Each variable was tested for a significant difference between landscapes with a Mann-Whitney *U*-test using a Bonferroni-corrected significance level of 0.05/24 ≈ 0.002.

The number of vegetation variables was further reduced to both avoid the problem of multicollinearity in regression analyses (Montgomery and Peck 1982) and to be able to

attach forest management significance to retained variables. This was achieved through a multivariate ordination approach. The results of an initial Detrended Correspondence Analysis of bird community response to vegetation suggested that a linear model was appropriate. Redundancy Analysis (RDA) is a direct ordination technique which uses a linear model of species response to environmental gradients (ter Braak 1987). Using the RDA routine of the software package CANOCO version 3.12 (ter Braak 1988*a*,*b*, 1990), I selected a reduced set of 12 vegetation variables which adequately described the variation in the vegetation data matrix, and had similar power for explaining variation in the bird data matrix as the original matrix of 29 variables (*i.e.* variables for which $t > 2.1$, ter Braak [1988*a*]).

3.2.3 Study Design and Data Analysis

The study was designed to assess the implications of different spatial perspectives in two ways: firstly by comparing patch-centred and landscape and analyses, and secondly by comparing analyses conducted at two levels of scale within aspen leave-areas only. Many sampling locations were used in more than one analysis at different scales by using a carefully designed subsampling strategy. In all cases, the spatial arrangement of census stations was matched as closely as possible between treatment and reference areas, and sampled stands were matched from forest inventory maps. The following sections and Fig. 3-1 outline the sampling design, along with the statistical analyses used for each question posed.

3.2.3.1 Question 1: Does fragmentation affect aspen forest songbird communities?

A total of 34 census stations sampled 13 aspen leave-areas (ranging in area from 3 to 45 ha) within a 1600 ha landscape in each of two years. Sampling in the reference landscape was done in equivalent sized areas of forest in a similar spatial distribution. This is representative of a typical sampling approach taken by most fragmentation studies: patch-centred and on a relatively small scale.

Species-area curves for each landscape in each year were plotted and the slopes of the two regression lines in each year were compared with ANCOVA. A repeated-

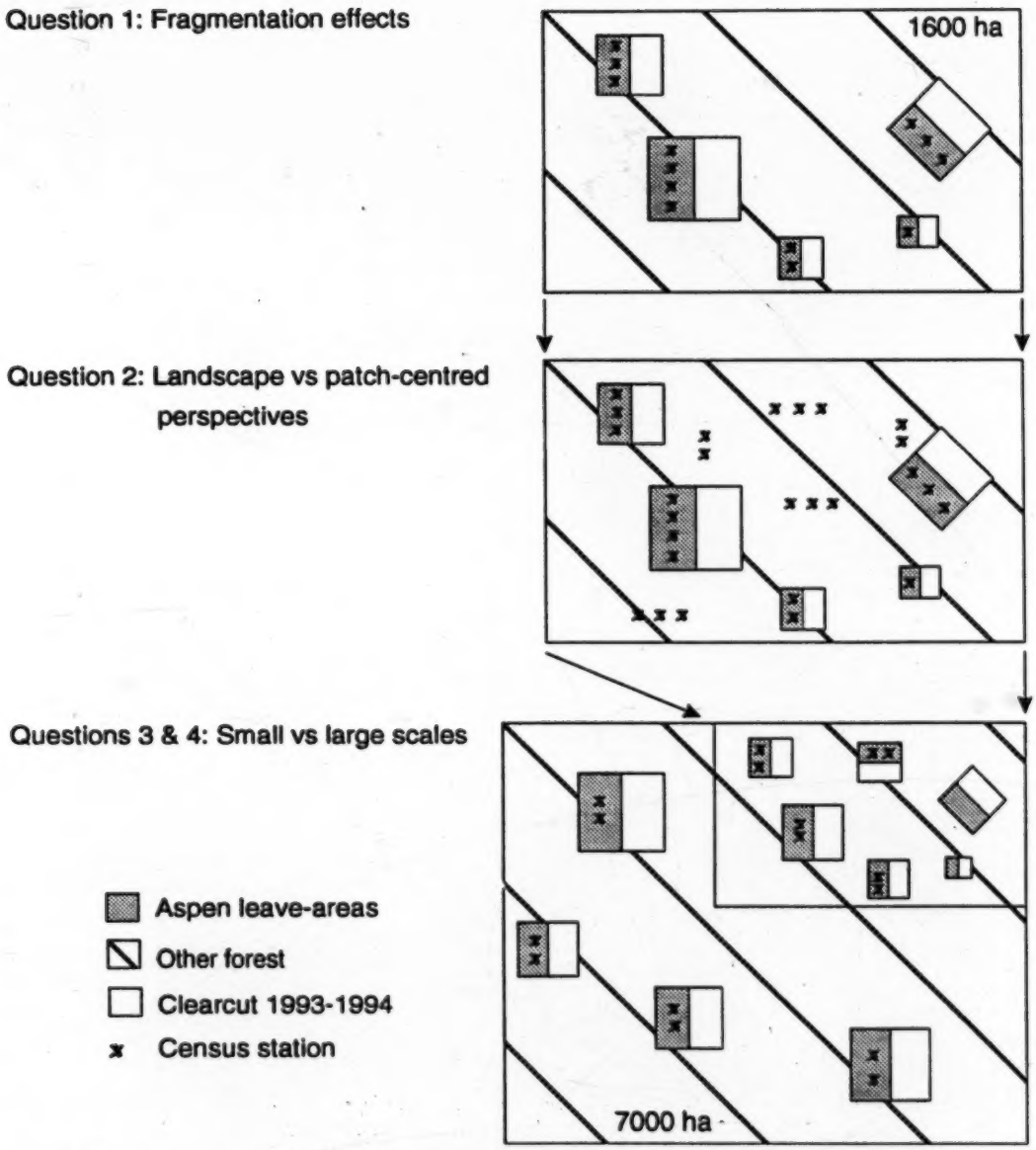

Figure 3-1: Schematic representation of study design showing the relationships between the sampling layout for each question. Aspen leave-areas were sampled in proportion to their area for the initial measurement of fragmentation effects (Question 1). Sampling locations were added in non-aspen forest to assess the importance of a landscape perspective (Question 2). Census stations were arrayed in pairs over the large scale to determine the impact of a larger spatial perspective (Questions 3 & 4).

measures ANCOVA was used to compare regressions across years (1994, 1995). Sampled areas were taken as 5 ha per census station, rather than actual leave-area size. ANCOVA was also used to compare regressions of species turnover between years as a function of area in the two landscapes. Turnover was measured using the Phi-squared index (Jackson *et al.* 1989). This index is based on a chi-square statistic normalized by total sample size, and is thus relatively insensitive to differences in sample size (Norušis 1994).

3.2.3.2 Question 2: Are effects of fragmentation still evident with an analysis of the whole landscape?

Within the same 1600 ha regions, 11 additional census stations were located in mixed aspen-spruce stands in 1994. In 1995, that number was raised to 15 to achieve sampling in proportion to the relative extent of mixed and pure aspen stands within the landscape. Pure conifer stands were very rare in these landscapes. The species composition of bird communities in aspen patches only, and in all forested sites were compared between landscapes using the Jaccard similarity index (Ludwig and Reynolds 1988), which does not include joint species absences and is not sensitive to variation in sample size.

Species occurrence patterns at aspen stations only and within all forested stations were compared to determine if differences between landscapes were consistent between patch-centred and landscape analyses. Nine species with >5 occurrences within each landscape were analyzed. Two species, Yellow-Rumped Warbler and Ovenbird, were sufficiently common to use a 50 m detection radius, and a 100 m radius was used for the others. Because local vegetation structure differed between landscapes (see below § *3.1 Results: Vegetation characteristics*), I first corrected for effects of local vegetation structure on the presence/absence of each species by building multiple stepwise logistic regression models. Residuals from these models were then used to compare the likelihood of each species occurring at a given sties between landscapes. All forested sites in both landscapes were used to generate the regression models, but only data from 1995 were used because not enough mixed forest sites were sampled in 1994. Vegetation variables

with highly skewed distributions were recoded into binary categorical variables (*high* versus *low*) prior to analysis. Model goodness-of-fit was assessed by examining standardized residuals, deviances and leverages, in addition to a test of significance (Hosmer and Lemeshow 1989), and extreme outliers were removed from analysis when required to obtain a satisfactory model fit (ter Braak and Looman 1987). Residuals from the regressions were compared between landscapes using Mann-Whitney *U*-tests because the residuals were not normally distributed when split by landscape. Significance levels were set at $\alpha = 0.1$ for all these analyses due to the relatively small sample sizes of mixed forest habitats.

3.2.3.3 Question 3: Are fragmentation effects consistent across spatial scales?

Songbird communities were sampled at two spatial scales in each of the treatment and reference areas. The approach taken was to maintain equal sampling effort at the two scales. In other words, a similar number of census stations was considered over each scale. (Note that the other possible approach of increasing the sample size with the area being considered would answer a different question of *sampling*, as opposed to *scaling*, effects). In each landscape the smaller scale was the 1600 ha region already described (see above § *2.3.1 Question 1*); the larger scale was a 7000 ha area which contained the 1600 ha region. Because a truly ecologically-based choice of scales was not apparent, the choice was based on units relevant to forest management practices. The large 7000 ha area constitutes most of one township (10 x 10 km); the township is currently the basic unit of forest harvest planning.

Thirty-four stations were analyzed at each scale. The smaller (1600 ha) scale analysis used the same 34 aspen stations previously described. At the larger (7000 ha) scale 2 stations from each of 17 aspen leave-areas were considered. Eight stations were subsampled in pairs from the smaller (1600 ha) area and 26 more stations were arrayed in 13 leave-areas across the remainder of the larger area.

Bird species richness and total bird abundance in aspen sites were tested for differences between landscapes at the two scales using a series of ANOVAs. Multiple stepwise linear regression was used to remove the influence of local vegetation structure

on richness and abundance data. Regressions were performed on each year's data separately. After ensuring satisfactory model fit, residuals were tested with ANOVA for the effects of scale and landscape, and their interaction (landscape x scale).

Species occurrence likelihoods were compared between landscapes at the two scales with an analysis analogous to that used for landscape data (see above § *3.2.3 Question 2*). Again only 1995 data were used, but in this case only aspen sites from both landscapes were used to generate regression models. Residuals from the regressions were tested for differences between landscapes with Mann-Whitney *U*-tests.

3.2.3.4 Question 4: Is there a biologically relevant scale to work at?

To determine if there was an inherent scale within the aspen bird communities examined, curves of cumulative species richness and species turnover (Phi-squared index) between years were examined for each landscape. An iterative algorithm was constructed to draw a site at random and to progress to all other sites following a nearest-neighbour criterion, while tracking cumulative species richness and turnover. The algorithm repeated until each site had served as the starting point and the average cumulative species richness and turnover were recorded. All aspen sites in each landscape were used. Graphs were drawn for the two scales in each landscape. Graphs were examined visually for horizontal asymptotes which might indicate that a threshold of scale had been reached, and the relative locations of asymptotes for the two landscapes were noted.

3.3 Results

3.3.1 Vegetation characteristics

Vegetation characteristics around point-count stations of aspen-dominated sites are summarized in Table 3-1. Large sample sizes result in a large number of variables showing a significant difference between landscapes. In some cases the absolute difference is quite small and of questionable biological significance, such as a 2.3 m difference in canopy height and a 3% difference in grass cover. However, the logged and reference areas differed in a few, potentially important, variables. The logged landscape had a significantly higher conifer component in aspen stands, as shown by higher values for coniferous tree and sapling densities, and higher subcanopy. The reference landscape

Table 3-1: Mean and standard errors of vegetation characteristics of aspen sites in logged and reference landscapes. Vegetation was measured at three 0.04 ha circular plots at each bird census station (n=74 for each landscape). Densities are given as stems/ha unless otherwise indicated; cover values are percentages. Differences between landscapes were assessed with Mann-Whitney *U* tests. The 12 variables retained for regression analyses are presented in **bold type**.

	Logged Landscape		Ref. Landscape		*U* statistic	Significance
Canopy						
Populus tremuloides density	547.5	(29.6)	524.3	(30.2)	2114.5	0.637
P. balsamifera **density**	44.4	(9.1)	104.7	(14.8)	1366.0	<0.001
Coniferous tree density	197.9	(26.6)	57.2	(12.3)	1129.5	<0.001
Other deciduous tree density	53.8	(13.2)	46.1	(10.3)	1942.5	0.203
Large snag density	97.2	(9.7)	110.9	(7.0)	1810.0	0.066
Small snag density	146.4	(9.2)	134.8	(9.5)	1924.0	0.185
Average snag diameter (cm)	16.6	(0.5)	16.0	(0.3)	1895.5	0.147
Average snag height (m)	15.7	(0.7)	15.9	(0.6)	2147.0	0.744
Canopy cover	78.9	(0.9)	80.7	(0.8)	1838.5	0.088
Canopy height (m)	22.0	(0.4)	24.3	(0.3)	1048.0	<0.001
Subcanopy						
Coniferous sapling density	309.8	(56.6)	124.2	(28.2)	1536.0	0.002
Populus **spp. sapling density**	564.8	(68.6)	789.4	(82.1)	1407.5	<0.001
Alder/willow sapling density	2427.4	(462.2)	1485.9	(273.4)	2121.5	0.656
Other sapling density	54.8	(11.7)	244.3	(36.1)	1063.5	<0.001
Subcanopy height (m)	8.0	(0.7)	3.2	(0.5)	1022.5	<0.001
Ground cover						
Shrub stem density (m^{-2})	1.7	(0.2)	3.0	(0.2)	1006.0	<0.001
Shrub cover	23.0	(1.7)	18.2	(1.1)	1725.5	0.027
All green cover	63.8	(1.9)	50.5	(1.6)	1116.0	<0.001
Forb cover	36.0	(1.6)	24.7	(0.9)	1016.0	<0.001
Grass cover	3.0	(0.4)	5.9	(0.7)	1322.5	<0.001
Dead grass cover	3.3	(0.6)	6.61	(0.9)	1356.0	<0.001
Moss cover	9.3	(1.8)	2.7	(0.8)	992.0	<0.001
Leaf litter cover	81.5	(2.0)	85.6	(1.1)	1907.5	0.162
Coarse woody debris cover	5.8	(0.4)	5.4	(0.3)	2064.0	0.485

tended to have greater numbers of balsam poplar trees and saplings associated with them.

Results of an initial Redundancy Analysis suggested that 12 of the 29 variables could be retained without significant loss of explanatory power (47.2% to 37.1% logged, 46.4% to 40.2% unlogged), and which were more manageable for regression analyses (bold type in Table 3-1). These 12 variables, describing primarily canopy and subcanopy structure, were used in regression analyses to remove the effect of local vegetation structure from bird data before analyses of species richness, bird abundance, and of individual species responses to fragmentation, as noted above.

3.3.1.1 Results of regression analyses

In this section I group the results of all analyses used to remove vegetation influence from bird data. Therefore, in all further discussions of bird data analyses this factor can be discounted.

With the landscape data set, vegetation variables significantly predicted the likelihood of bird species occurrence in 8 out of 9 logistic regression models (Table 3-2). The occurrence pattern of the Tennessee Warbler could not be predicted with any of the 12 vegetation variables used in model building. Overall classification success ranged from 61.9% to 83.0% and all models were highly significant ($p < 0.001$). A maximum of 4 outlying points was removed from any given model after one or two initial regressions. The density of coniferous trees was the most significant predictor variable in all models; the density of aspen and willow saplings and trees were present in 4 out of 8 models.

The results of the regressions using aspen sites only were qualitatively similar, and are not presented in detail here (see Appendix 3). Classification success ranged from 58.8% to 83.3%, and all models were highly significant. Variables describing the coniferous content of patches were again present in all 10 models, and the densities of aspen and willow saplings and trees were present in 6 models.

Multiple linear regression analyses were used to remove vegetation influences from measures of species richness and bird abundance before analyzing them for differences between scales (see Appendix 3). Variables describing coniferous content of aspen stands along with the density of alder and willow were once again the most important variables in

Table 3-2: Logistic regression models describing the influence of local vegetation structure on the probability of occurrence of 8 bird species. Occurrence was measured on a per-census-station basis with a detection radius of 100m except where noted. Model goodness-of-fit is given by the percentage of stations correctly classified, the model chi-squared value, and an associated probability. All tree and sapling variables are densities.

CT - Coniferous trees
PT - *Populus balsamifera* trees
AWT - *Alnus* spp. & *Salix* spp. trees
CSap - Coniferous saplings
PSap - *Populus* spp. saplings
AWSap - *Alnus* spp. & *Salix* spp. saplings
OSap - Other saplings
SSnag - Small snags (8-12 cm dbh)
LSnag - Large snags (>12 cm dbh)
CHt - Canopy height (m)
SCHt - Subcanopy height (m)
CCov - Canopy cover (%)

Species	Model[a]	% Correct		Model χ^2	p
		Presence	Absence		
Swainson's Thrush	1.517 + 0.838CT - 0.845LSnag - 0.544CCov + 1.302CHt - 0.785AWT - 0.869 CSap	83.1	78.4	46.97	<0.001
Red-Eyed Vireo	-0.307 - 3.151CT	86.5	78.6	49.67	<0.001
Yellow-Rumped Warbler[b]	0.046 + 0.803CT + 0.506CCov	54.2	69.4	13.09	0.001
Connecticut Warbler	-1.399 - 1.957CT + 1.631SSnag - 0.57OSap + 0.745 AWSap + 0.975PT	77.5	88.9	58.25	<0.001
Mourning Warbler	-0.208 - 1.687 CT + 0.9CHt - 0.703 AWSap + 0.545AWT	76.6	70.6	36.21	<0.001
Ovenbird[b]	-0.671 - 0.431CT + 0.569CCov + 0.77SCHt + 0.77PT + 0.433PSap	68.9	73.1	29.53	<0.001
White-Throated Sparrow	0.984 - 0.795CT + 1.353OSap - 0.739PT - 0.564AWT - 0.628PSap	80.8	80.4	42.22	<0.001
Chipping Sparrow	1.00 + 2.387CT	76.8	74.4	30.87	<0.001

[a] Expression given is for Z where Prob(presence) = $1/(1 + e^{-Z})$
[b] Detection radius of 50 m used.

the models. All models were highly significant ($p \leq 0.001$), but explained variances were very low, with adjusted r^2 values ranging from 0.12 to 0.25.

3.3.2 Question 1: Fragmentation effects

Several species characteristic of 'open' habitats were detected only in aspen forest patches adjacent to clearcuts in the logged landscape, including Brown-Headed Cowbird, House Wren, Alder Flycatcher, Western Wood-Pewee, Eastern Phoebe, and Clay-Coloured Sparrow (for total number of detections and scientific names see Appendix 2). These species were always detected at greater distances from observers (> 100 m) and were likely using the edges of leave-areas, or the cutblocks themselves. Total species richness across the whole landscape was thus higher in the logged area (45 species) than in the reference (36 species).

Species-area relationships for aspen forest songbirds were significant with explained variances between 54.4% and 73.5%. Relationships did not differ between logged and reference areas in either 1994 or 1995 (Fig 3-2; 1994: $F = 2.05$, $p = 0.17$; 1995: $F = 0.93$, $p = 0.34$), and the regressions did not change between years (logged: $F = 0.11$, $p = 0.75$; reference: $F = 0.56$, $p = 0.47$). Removal of 'open' habitat species (following general habitat descriptions in Semenchuk [1992]) from the analysis did not significantly change the results.

There was a significant negative relationship between species turnover between years and area (Fig. 3-3; $F = 78.54$, $p < 0.001$), although considerable scatter in the data resulted in low explained variances (logged adj. $r^2 = 0.37$; reference adj. $r^2 = 0.61$). The slope of the relationship of turnover to patch area was not different between logged and reference areas ($F = 0.12$, $p = 0.73$). Higher turnover in the logged landscape was mostly a result of a higher incidence of species additions to patches (Table 3-3). These additions were not species particularly characteristic of 'open' habitats. Three species, Yellow-Bellied Sapsucker, Hermit Thrush, and Swainson's Thrush, appeared to have declined in the reference area while increasing in the logged landscape. Red-Breasted Nuthatch was the only species to decline significantly in the logged area while increasing in the reference.

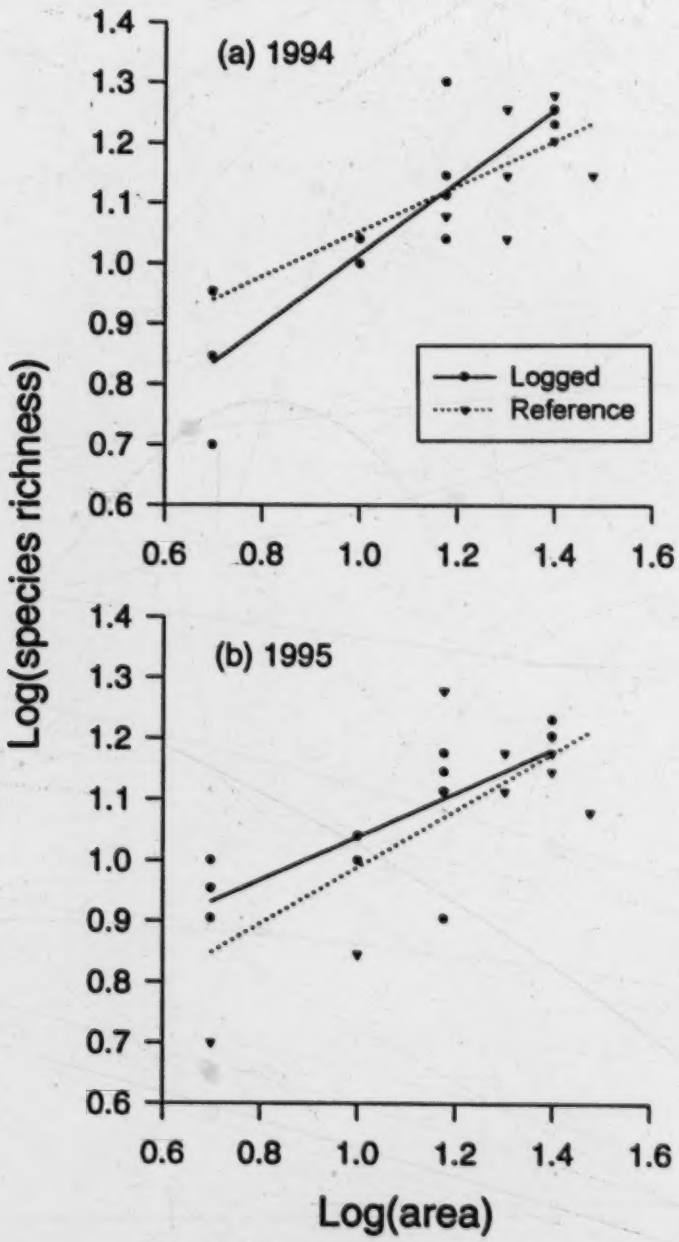

Figure 3-2: Species-area relationships for all species of songbirds in aspen forest in logged and unlogged (reference) landscapes in (a) 1994 and (b) 1995, representing 1 and 2 years post-logging. Regressions are not different between logged and reference landscapes, nor between years. Area was measured in hectares at 5 ha per census station.

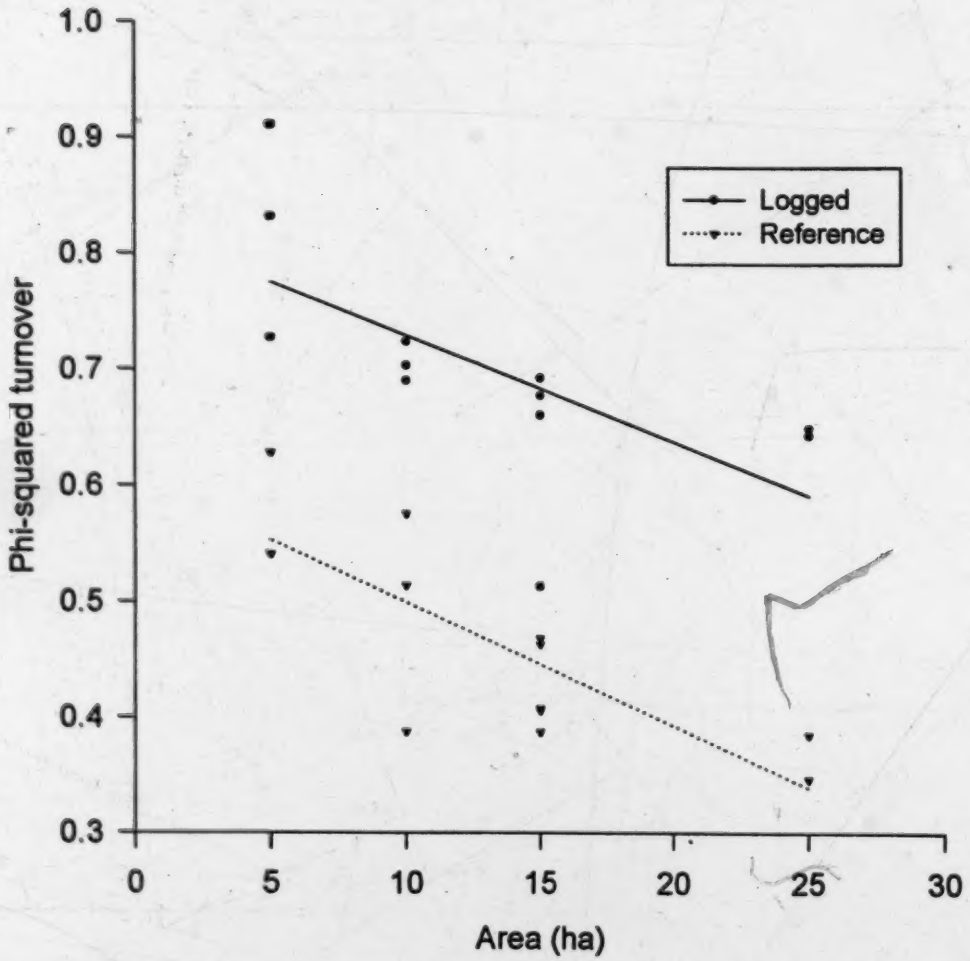

Figure 3-3: Relationships of songbird community turnover in aspen forest patches to patch area in logged and unlogged (reference) landscapes. Sampling intensity was 1 census station per 5 ha of forest. Turnover is significantly higher in the logged landscape ($p < 0.001$) although the slopes of the relationships are not different between landscapes.

Table 3-3: Species responsible for community turnover from 1994 to 1995. Species with ≥3 incidences of loss or gain at the patch (leave-area) level between years are shown with the number of patches from which they were lost, or to which they were added in 1995. Total number of patches was $n = 13$ (logged landscape) and $n = 11$ (reference landscape).

Species lost	(# patches lost from)	Species gained	(# patches gained in)
Logged landscape			
Red-Breasted Nuthatch	(7)	Tennessee Warbler	(5)
Western Tanager	(5)	Hermit Thrush	(5)
Solitary Vireo	(3)	Yellow-Bellied Sapsucker	(5)
Mourning Warbler	(3)	Gray Jay	(4)
Lincoln's Sparrow	(3)	Dark-Eyed Junco	(3)
		Winter Wren	(3)
		Least Flycatcher	(3)
		Warbling Vireo	(3)
		Swainson's Thrush	(3)
Total losses[a]	46	Total gains[a]	55
Reference landscape			
Red-Breasted Nuthatch	(4)	Tennessee Warbler	(5)
Rose-Breasted Grosbeak	(3)	Gray Jay	(4)
Swainson's Thrush	(3)	Red-Breasted Nuthatch	(3)
Yellow-Bellied Sapsucker	(3)		
Black-Thr. Green Warbler	(3)		
Hermit Thrush	(3)		
Lincoln's Sparrow	(3)		
Total losses[a]	48	Total gains[a]	37

[a] Total number of gains and losses was defined as the total number of cases of loss or gain of any species in any patch.

3.3.3 Question 2: Patch-centred vs. landscape analyses

Bird communities were more similar between landscapes when all forested habitats were included, than with aspen patches only. In 1994, the Jaccard similarity index between landscapes increased from 0.70 to 0.80 when mixed aspen-spruce habitats were included. In 1995, with a more balanced sampling intensity, the Jaccard index increased from 0.68 to 0.87 when mixed habitats were added to the analysis.

A landscape perspective significantly altered the interpretation of occurrence patterns compared between logged and reference areas for 3 species (Table 3-4). Yellow-Rumped Warblers showed no difference between landscapes with a patch-centred analysis, but were significantly more likely to occur in the logged landscape with a landscape analysis. Mourning Warblers appeared more likely to occur in the reference landscape only with a landscape analysis. With a patch-centred view Ovenbirds appeared more likely to occur in the logged landscape, but this difference disappeared with a landscape view. Two species (Tennessee Warbler, White-Throated Sparrow) were more likely to occur in the reference landscape by either analysis. The remaining four species showed no significant difference between landscapes.

3.3.4 Question 3: Effect of spatial scale in aspen patches

Spatial scale had a significant effect only in the reference landscape in 1995 on both bird species richness (Table 3-5) and total bird abundance (Table 3-6) at each census station. Species richness did not change with the landscape nor with scale in 1994, but there was a significantly ($p = 0.04$) lower species richness at the larger scale in the reference landscape in 1995. The trend across scales was in opposite directions in the two landscapes in both years. In the logged landscape, species richness was slightly higher at the larger scale, while in the reference landscape the reverse was true. Absolute differences in species richness between scales were quite small in all cases, and ranged from 0.23 to 1.41 species per station.

Mean total bird abundance differed significantly between scales in the reference landscape (Table 3-6). Although the scale effect was present in both years, it worked in the opposite direction in 1995 compared to 1994. Significantly higher abundances were

Table 3-4: Summary of tests of species occurrence probabilities between logged and reference landscapes within aspen sites only and across all forested sites. Tests were Mann-Whitney *U*-tests on the residuals of logistic regressions of species occurrence probabilities, except where noted. Sample sizes are given as the degrees of freedom (df) from the Mann-Whitney tests for (logged landscape, reference landscape). Detection radius was 100 m except where noted.

Species	Aspen sites only				All forest sites			
	U	df	*p*	Compared[a]	*U*	df	*p*	Compared[a]
Swainson's Thrush	523.0	(33,34)	0.634		1088.0	(48,48)	0.639	
Red-Eyed Vireo	423.0	(31,33)	0.233		1033.0	(46,48)	0.591	
Yellow-Rumped Warbler[b]	509.0	(33,34)	0.514		921.0	(48,49)	0.066	Logged ↑
Tennessee Warbler[c]	391.0	(34,34)	0.005	Reference ↑	833.0	(49,49)	0.002	Reference ↑
Connecticut Warbler	454.0	(31,34)	0.338		1012.0	(45,49)	0.493	
Mourning Warbler	457.0	(34,34)	0.138		889.0	(49,49)	0.027	Reference ↑
Ovenbird[b]	363.0	(34,33)	0.013	Logged ↑	1002.0	(49,48)	0.209	
White-Throated Sparrow	217.0	(33,34)	<0.001	Reference ↑	821.0	(46,49)	0.023	Reference ↑
Chipping Sparrow	498.0	(32,34)	0.555		1042.5	(46,49)	0.529	

[a] Indicates for which landscape the likelihood of occurrence was higher for cases where the difference was at least marginally significant ($p \leq 0.1$).
[b] Detection radius of 50 m used.
[c] No significant regression model could be built; tests were performed on raw presence/absence data.

Table 3-5: Mean total bird species richness per census station (standard error) at two scales of sampling in logged and unlogged reference areas. All significance levels were assessed using ANOVA. Effects of vegetation on bird species richness were first removed using multiple stepwise linear regression separately for each landscape; ANOVAs were calculated on the unstandardized residuals from the regressions.

Landscape	Scale	1994				1995			
		Richness	*n*	Scale Effect	Trt Effect	Richness	*n*	Scale Effect	Trt Effect
Logged	Small	7.85 (0.30)	34	F=0.046 p=0.830		6.64 (0.31)	34	F=0.107 p=0.745	
	Large	8.08 (0.34)	26		F=0.051 p=0.822	7.30 (0.35)	33		F=1.217 p=0.272
Reference	Small	8.00 (0.40)	31	F=0.703 p=0.405		7.50 (0.34)	34	F=4.471 p=0.038	
	Large	7.45 (0.30)	20			6.09 (0.29)	34		
				Trt x Scale F=0.012 p=0.914				Trt x Scale F=4.054 p=0.046	

Table 3-6: Mean total bird abundance per census station (standard error) at two scales of sampling in logged and unlogged reference areas. All significance levels were assessed using ANOVA. Effects of vegetation on bird abundance were first removed using multiple stepwise linear regression separately for each landscape; ANOVAs were calculated on the unstandardized residuals from the regressions.

Landscape	Scale	1994				1995			
		Abundance	*n*	Scale Effect	Trt Effect	Abundance	*n*	Scale Effect	Trt Effect
Logged	Small	10.21 (0.42)	34	F=0.020 p=0.889		8.46 (0.46)	34	F=0.828 p=0.366	
	Large	11.21 (0.45)	26		F=3.604 p=0.060	9.50 (0.53)	33		F=1.659 p=0.200
Reference	Small	11.64 (0.56)	31	F=4.204 p=0.046		9.99 (0.52)	34	F=3.473 p=0.067	
	Large	13.55 (0.86)	20			7.94 (0.38)	34		
				Trt x Scale F=2.900 p=0.091				Trt x Scale F=3.841 p=0.064	

seen at the larger scale in 1994 ($p = 0.05$), but the trend reversed in 1995 ($p = 0.07$). No significant effect was seen in the logged landscape, but the trend was towards higher abundances at the larger scale. Additionally, the logged landscape had significantly lower bird abundances than the reference in 1994 ($p = 0.06$).

Six out of 10 species analyzed showed scale-dependence in tests of their occurrence likelihoods between logged and reference landscapes (Table 3-7). Two species, Yellow-Rumped Warbler and Ovenbird, only exhibited a difference with a large scale analysis, while the other 4 species only differed at the small scale. The direction of the differences was not consistent, with 3 species appearing more likely to occur in each of the logged and reference landscape.

3.3.5 Question 4: Is there an inherent scale?

Curves of species accumulation did not possess a distinct asymptote and instead climbed continuously but less steeply (Fig. 3-4). The shape of all curves was well described with a simple power function $y = ax^b$. All curves climbed steeply for the first 10 census stations, at which point differences between landscapes and/or scales became apparent. Curves from both landscapes and scales had similar shapes, with differences evident mostly in the total number of species present. Between 19 and 28 stations were required to detect 90% of species; no trend was evident for differences between landscapes or scales.

A threshold of bird community turnover with spatial scale (sample size) was observed in the logged landscape, but not the reference landscape (Fig. 3-5). Turnover declined with increasing spatial scale in both logged and unlogged landscapes, but reached a distinct minimum only in the logged landscape. A minimum turnover value of 0.33 was reached with roughly 20 stations in the analysis at both small and large scales in the logged landscape, although this asymptote is less evident at the large scale due to a smaller sample size. Turnover in the logged landscape remained higher than in the unlogged landscape at all scales. Turnover in the unlogged landscape declined to roughly 0.25 (25% lower than in the logged landscape), and appeared not to have levelled off within the range of scales (sample sizes) considered in this study.

Table 3-7: Summary of tests of species occurrence probabilities between logged and reference landscapes at small and large scales within aspen sites. Tests were Mann-Whitney *U*-tests on the residuals of logistic regressions of species occurrence probabilities. Sample sizes are given as the degrees of freedom (df) from the Mann-Whitney tests for (logged landscape, reference landscape). Detection radius was 100 m except where noted.

Species	Small scale				Large scale			
	U	df	*p*	Compared[a]	*U*	df	*p*	Compared[a]
Least Flycatcher	393.5	(32,34)	0.054	logged ↑	473.5	(32,33)	0.473	
Swainson's Thrush	382.0	(34,34)	0.016	reference ↑	521.0	(33,34)	0.616	
Red-Eyed Vireo[b]	459.0	(32,34)	0.365		442.0	(30,34)	0.136	
Yellow-Rumped Warbler[b]	537.0	(33,34)	0.763		374.0	(32,33)	0.043	reference ↑
Tennessee Warbler	477.0	(34,34)	0.192		521.0	(33,34)	0.591	
Connecticut Warbler	401.0	(32,33)	0.096	logged ↑	477.5	(31,32)	0.799	
Mourning Warbler	375.0	(32,33)	0.045	reference ↑	550.0	(33,34)	0.890	
Ovenbird[b]	499.0	(34,34)	0.330		375.5	(33,34)	0.019	logged ↑
White-Throated Sparrow	514.0	(34,34)	0.432		502.0	(33,34)	0.459	
Chipping Sparrow	478.0	(34,30)	0.667		429.0	(32,33)	0.194	

[a] Indicates for which landscape the likelihood of occurrence was higher for cases where the difference was at least marginally significant ($p \leq 0.1$).
[b] Detection radius of 50 m used.

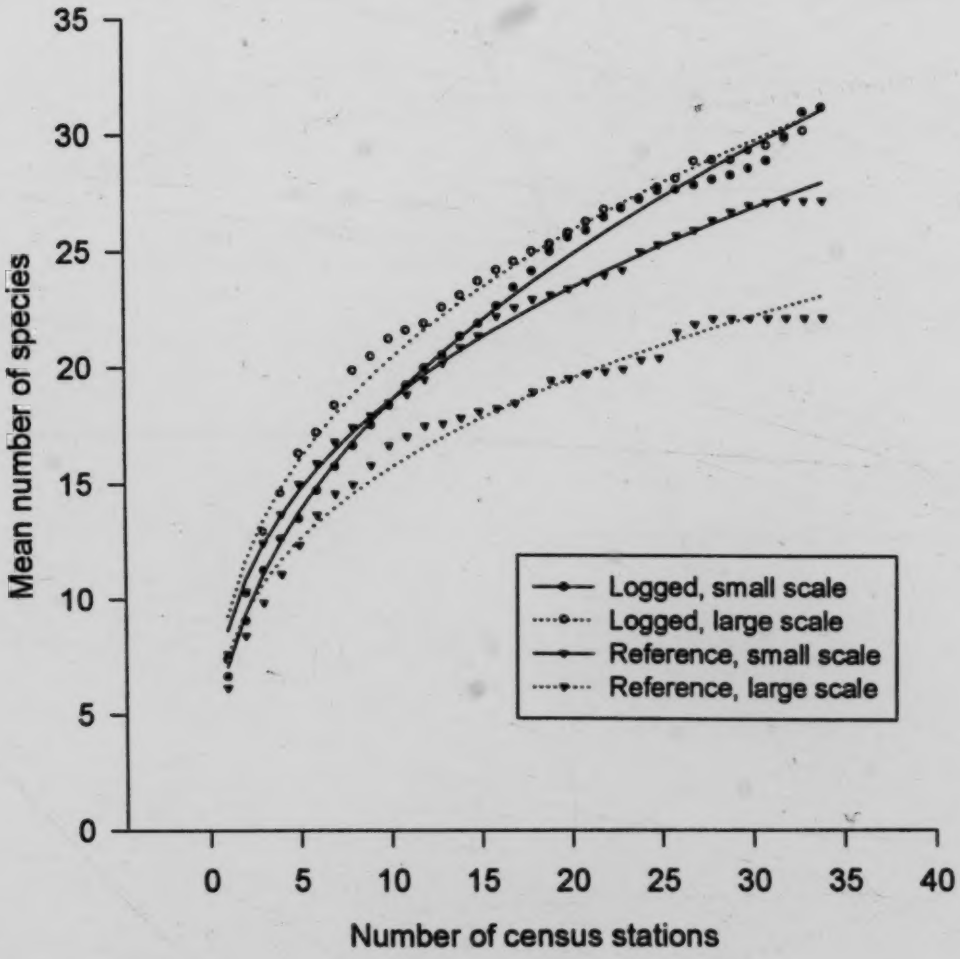

Figure 3-4: Species accumulation curves produced at two spatial scales in logged and unlogged (reference) landscapes. Census stations were added following a nearest-neighbour criterion. Fitted curves are simple power functions $y = ax^b$.

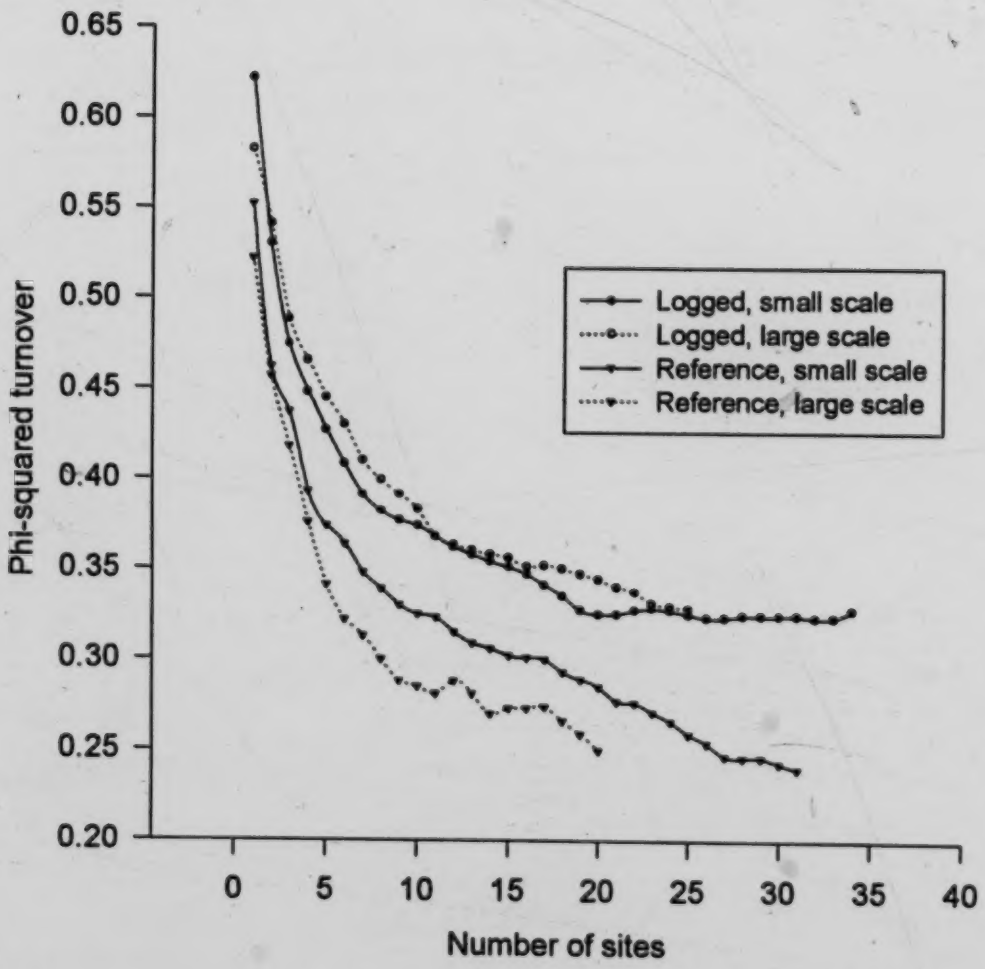

Figure 3-5: Curves of phi-squared turnover of bird communities between 1994 and 1995, calculated with increasing sample sizes. Census stations were added following a nearest-neighbour criterion, and Φ^2 was recalculated with the total sample at each step.

3.4 Discussion

This study posed a series of questions related to the potential importance of spatial perspective in studies of songbird response to habitat fragmentation. The intent was to establish the response of songbirds to landscape fragmentation by clearcut logging at the spatial scale that such studies are typically conducted, and then to investigate how our interpretation of those responses might vary given different scales of analysis. Patches were firstly considered in a wider landscape perspective, and secondly were analyzed over a larger scale.

Species-area relationships were not different between logged and unlogged landscapes, however rates of community turnover were higher in the fragmented landscape at the small scale. Total species richness was higher in the logged landscape due to the presence of species characteristic of more open habitats there. The occurrence likelihoods of 3 out of 8 species were found to be dependent on whether a patch-centred or landscape view was used in analyses. Additionally, community similarity between logged and unlogged landscapes was higher when all forested sites were considered. Within the aspen component of the landscape, scale-dependence was observed in the measurement of bird species richness and abundance, and in the occurrence likelihoods of 6 out of 10 species. However, these effects were not consistent across years nor in their direction of influence.

3.4.1 Study design and vegetation influences

An important distinction must be made clear in interpreting the results of this study. The two main questions dealing with issues of spatial scale represented fundamentally different approaches to the scale problem. In addressing the issue of patch-centred versus landscape views of the bird community, the question was really one of sampling effort. What effect did increased sampling effort over a greater proportion of the landscape have on the interpretation of fragmentation effects? The sampling design used to address this question technically did not change the scale of the study, but did change the focus and intensity of sampling by adding census stations in habitats which would typically be considered 'matrix' (Wiens 1994).

This sampling question was conceptually different from the question posed in assessing the effects of scale within the aspen component of the landscape. Here the focus was on true scaling effects with an equal number of census stations distributed at two distinct scales. While it may be possible to define an appropriate scale for the study of an individual species on the basis of the species' natural history (Addicott *et al.* 1987), the appropriate scale for studying an entire animal community is less clear. Such a scale may not even exist, with different properties and behaviours emerging at each new level of scale (O'Neill *et al.* 1986), or domains of scale may exist within which patterns are consistent (Wiens 1989a). It is likely not possible to know *a priori* which of these scenarios holds for a particular system, thus necessitating a multi-scale approach such as that taken by this study.

The logged (treatment) and unlogged (reference) landscapes chosen for study were matched for the proportions of different stand types they contained, and only similar stands (in terms of age and canopy composition) were sampled based on forest inventory maps. However, on analysis of the detailed vegetation data collected in this study, several differences in local vegetation structure became apparent nonetheless. It is well known that local scale vegetation structure can influence bird abundances, species richness, and community diversity (Boecklen 1986, Freemark and Merriam 1986). The regressions used to remove local vegetation influence incorporated only those data from the census stations considered for each analysis (*i.e.* different sets of bird and vegetation data generated the models for the landscape and aspen scaling analyses). This approach more accurately reflected the two alternative scenarios for study design under consideration and avoided confusing the issues of scaling and sampling within each question. In two-stage analyses of this sort it is implicitly assumed that the factors are independent; in the present case this means that interactions between vegetation structure and scale are assumed to be negligible. There are further concerns about the use of residuals from a logistic regression (as opposed to the linear case), but the results are likely to be biologically meaningful (T. Taerum[1], pers. comm.). The fact that the vegetation variables of greatest concern

[1] Dr. Terry Taerum, Statistics Consultant, Computing and Network Services, University of Alberta.

consistently entered into regression models suggests that these analyses were successful in removing inherent biases from the data in the two landscapes.

3.4.2 Question 1: Fragmentation effects: patch-centred view

Both species richness and community turnover varied significantly with area, but only turnover differed between landscapes. Species-area curves in logged and reference landscapes were similar in both years. This result differed from expectations of steeper slopes and lower intercepts in the logged landscape based on predictions derived from island biogeographic theory and studies in eastern North America. However, the same result was observed in a study conducted in a neighbouring area (Schmiegelow *et al.* In press). Most studies which have documented community collapse have been conducted in areas where fragmentation occurred many years previously. The area considered by the present study was fragmented only the winter prior to the first season of data collection, and it is thus possible that some effects may only be detectable over a longer time period. Additionally, fragmentation may have occurred at a scale closer to that of the individual bird, rather than at the population level (Andrén 1994) making the application of island biogeographic theory questionable. However, turnover was higher in the logged landscape, a result again consistent with Schmiegelow *et al.* (In press). Although there was no significant reduction in species richness, considerable replacement of species occurred. The pattern was towards more frequent losses of older-forest species and more frequent gains of younger-forest species, based on species preferences identified by Schieck *et al.* (1995). If this trend were to continue, older-forest species could decline significantly in this area.

The increased species richness over the whole logged landscape is not surprising, and has been observed elsewhere (*e.g.* McGarigal and McComb 1995). While cutblocks may be uninhabitable by forest-dwelling species, they provide suitable habitat for some species. Attention has previously been given to the invasion of new species into recently fragmented areas (*e.g.* Brittingham and Temple 1983). Of the species observed only in the logged landscape aspen patches, only two (Brown-Headed Cowbird and House Wren) were not sighted elsewhere in the study area. All other species apparently invading the

logged landscape had in fact been detected in other habitats, especially fens and other wetland areas (M. Norton unpublished data). Most of these 'invasions', then, are probably better thought of as local-scale expansions into newly created habitats, or as spatial redistributions.

3.4.3 Question 2: Significance of landscape sampling

The occurrence likelihoods of three species tested between landscapes (Yellow-Rumped Warbler, Mourning Warbler, Ovenbird) changed significantly with a landscape analysis over a patch-centred analysis. The nature of this influence was not consistent across species, however, with the first two species showing a difference between landscapes only with a landscape analysis, the latter showing no difference only at that scale.

The main focus of the landscape question, as with the aspen scaling question discussed in the next section, was at the individual species level. The potential that a given species would exhibit a different pattern over an entire landscape than in a more habitat specific analysis is, of course, a function of the variation in habitat that can be utilized by that species. That is, a species whose suitable habitat includes only aspen stands would not be expected to have a different pattern when all forested sites are included. Conversely, in the case of a species that is able to use a wider range of habitats, a study including only a portion of those habitats would not get a total picture of what is occurring in that population. After fragmentation by logging, some of these latter species may, at the local level, be able to compensate for loss of one habitat type by shifting population density towards another habitat type, similar to the process of landscape supplementation hypothesized by Dunning *et al.* (1992). It should be emphasized here that aspen fragments in an industrial forest landscape are not habitat islands in the sense of a patch of forest in a non-forest matrix, such as in an agricultural setting (*e.g.* Merriam 1988). In the boreal landscape of northern Alberta much other forest remains after logging since forest companies typically harvest only one stand type.

Most species of boreal songbirds naturally include a range of vegetation in their habitat (Welsh and Lougheed 1996). The two species (Yellow-Rumped Warbler,

Mourning Warbler) which were found to exhibit a different pattern at the landscape scale only are among those with a wide range of habitat usage (Welsh and Lougheed 1996), being common in both deciduous and mixed stands. Ovenbirds, too, were observed in a variety of stand types in this study. These are species, then, for which a focus on aspen patches may not be appropriate. Only when all relevant habitats are included can conclusions be made about the response of any given species to fragmentation. Comparisons among species should not be made unless comparable proportions of their habitats are considered. Thus, from this study, one would conclude that Mourning Warbler, Tennessee Warbler, and White-Throated Sparrow appear to be negatively affected by fragmentation (Table 3-4).

Throughout this study the definition of 'habitat type' has been based on the age and canopy composition classes of existing forest vegetation mapping. This is the sort of anthropocentric bias that has been recognized earlier as an important problem to overcome in ecological research (Addicott *et al.* 1987, Morris 1987). In a recent study by Knight and Morris (1996) the authors provided dramatic evidence of this by showing that a population of voles (*Clethrionomys gapperi*) responded neither to the 2 habitats recognized by the researchers, nor to the 7 habitats classified by remote sensing, but to *3* classes. The results obtained in the present study also suggest that human-defined habitats may not be relevant to the organisms under study.

3.4.4 Question 3: Spatial scale in aspen patches

Species richness and total bird abundance were found to vary with spatial scale only in the reference landscape, and the direction of the effect was different in each year. Additionally, the apparent response to fragmentation of 6 out of 10 species differed with spatial scale. At the small scale 4 species were more likely to occur in one landscape than the other, and at the large scale these differences disappeared, and 2 other species showed a difference.

Without an identification of the particular processes by which habitat fragmentation affects a particular species, it is impossible to explain why certain species respond only at a smaller scale, and others only at a larger scale. It could be connected

with body size, with larger species more appropriately viewed at a larger scale, although the suite of species encompassed by this study fall into a fairly narrow range of body sizes. Alternatively, different species may be affected by different processes associated with fragmentation that are dominant at slightly different scales. This study was not designed to assign cause-and-effect to observed patterns, but simply to determine to what degree scale-dependence may influence studies in fragmented habitats. Without further replication or an even wider range of scales it is difficult to say which of the results presented are "real" scale effects and which might be artifacts of sampling or analysis.

Scale-dependence has been found in previous studies of avian ecology (*e.g.* Wiens *et al.* 1987, Blake *et al.* 1994). Typically, the scale ranges considered have been greater than in the present study and have variously encompassed everything from individual breeding territories to a biogeographic scale. Regardless, at the community level of investigation any scale chosen will, to some extent, be observer biased due to problems of community boundary definition and process identification. As shown here, even relatively smaller changes in scale may be accompanied by apparent differences in patterns. A hierarchical approach can help determine at what scales the effects of fragmenation are best understood (Kotliar and Wiens 1990). Birds likely vary in the scale at which they respond to induced patchiness, just as they do to natural patchiness.

As an additional note, the 'small scale' tests in the aspen scaling analysis (Table 3-7) can be compared to the 'aspen sites only' tests in the landscape analysis (Table 3-4). Seven out of 9 species common to both analyses exhibit a different response by each test. This does not negate the relevance of the two analyses, but does prevent any firm conclusions as to whether a given species is negatively affected by fragmentation. As an example, Yellow-Rumped Warbler might show a negative response, a positive response, or no response to fragmentation depending on the scale and habitats considered. This is sharp evidence that bird-habitat relationships must be carefully defined, as must a relevant spatial scale, before drawing conclusions from large scale studies. It is often not possible to obtain the sample sizes necessary to average out variation in bird-habitat relationships when working at large scales (Wiens *et al.* 1987), making study design a particularly

critical step in research. Data collection over a longer time span is also necessary as temporal variation may also be scale-dependent (Blake *et al.* 1994) and could further complicate interpretation of results.

If different measures indicate different responses with different scales it calls into question how an 'impact' is determined. Given the scale-dependency of both community- and population-level data, it may be necessary to investigate the responses to fragmentation at yet wider ranges of scale to include both finer (individual based) and broader scales as well. Several authors have advocated the need to design ecological studies at a scale relevant to the organism of interest, and conceptual models for how to do this have been proposed (Addicott *et al.*1987, Morris 1987). However, defining a scale relevant to a particular population or community is a more daunting task, and as yet few models have been developed (although see Holling [1992] for a noble attempt). This has led many authors (*e.g.* Wiens *et al.* 1987, Virkkala 1991), including this one, to advocate multi-scale approaches.

3.4.5 Question 4: No evidence for a threshold of scale?

Curves of cumulative species richness and turnover do not strongly suggest that there is any definitive threshold of scale in boreal bird communities over the range of spatial scales encompassed by this study. The lack of a horizontal asymptote in either graph suggests that community patterns, here measured by species richness and turnover, will be interpreted differently depending on the spatial extent of the study. The one exception might be cumulative turnover in the logged landscape which did appear to level off after roughly 25 census stations.

It is not clear whether ecological systems should be expected to exhibit clear thresholds of scale. Many authors hold that scale-dependent phenomena are simply an artifact of the scales of measurement (Allen and Starr 1982), while others maintain that there are inherent scales (Morris 1987, Carlile *et al.* 1989). One of the earliest attempts at quantifying natural ranges of scale was to generate species-area curves over increasing plot sizes (*e.g.* Greig-Smith 1964). That is essentially the approach taken here, and while the measure is somewhat crude, the fact that new species were still being added at 35

census stations suggests that no threshold for this measure had been reached. The difference between the large and small scales in the reference landscape is largely due to vegetation differences between stands sampled at each scale. Some sampling locations at the small scale were located in stands with enough balsam poplar and associated shrubs to increase bird species richness. Both lines increase steadily nonetheless, indicating that the trend is independent of local vegetation.

The observation that communities appear more stable over larger areas is not a new one (Connell and Sousa 1983, Wiens 1989*b*), and in fact the turnover-area relationship presented earlier is partly an illustration of that. However, the question of interest here is whether a threshold exists beyond which no increase in stability is observed. That is definitely not the case in the reference landscape because turnover continued to decline over the full range of sample sizes. Conversely, it appears that in the logged landscape a threshold was indeed reached. This could be evidence of a large-scale change in a community structuring process after fragmentation, but the data collected in this study do not allow any interpretation of the process(es) which might be responsible.

A question worthy of further consideration is the relationship between the spatial structure of bird communities and that of forest vegetation. This is of relevance in determining the degree of spatial autocorrelation in bird community patterns. In a situation with a significant amount of spatial structure in bird communities, independent of vegetation structure, studies conducted at too small a scale might generate spurious results because of spatially autocorrelated data (Legendre 1993). Based on a series of direct ordinations, this does not appear to be a severe problem in these data sets, but there is some evidence for altered spatial structures in bird communities in the logged landscape (see Appendix 1).

Both of these last two results suggest that only large reserves of uncut forest will successfully conserve all patterns in bird communities. While many species would likely be represented in smaller areas, my analyses of 7000 ha areas indicate that there are large scale patterns of community turnover and spatial structure which would only be maintained in large regions. Given our present level of ignorance about the role that these

might play in long-term community function, the only prudent conservation strategy would be to plan for large reserve areas. Further research should address the function of large scale phenomena.

3.5 Conclusions

Few effects of fragmentation due to clearcut logging were conclusively documented, especially when compared to the magnitudes of effects observed in eastern North America. Hansen and Urban (1992) have hypothesized that bird communities in different biomes may respond differently to landscape change. The suggestion has been made that boreal forest ecosystems may be more resilient to anthropogenic disturbances because of the major historical role of large natural disturbance events, such as fire (Hansson and Angelstam 1991, Schmiegelow *et al.* In press). As a result, boreal birds may be somewhat resilient to major disturbances.

Before any conclusions are made, however, a few caveats should be mentioned. Firstly, only very broad community indices were used in analyses and more subtle effects in terms of reproductive success would therefore not have been detected. The short time span of the study, the fact that forests were only very recently fragmented and the large expanses of intact forest remaining nearby all combine to prevent any longer-term predictions. As logging proceeds, short-term trends may become significant, or critical thresholds may be reached beyond which significant problems arise. Cumming *et al.* (1994) have predicted conflicts between forestry and wildlife in northern Alberta over a longer time span.

What is clear from the results presented here is that spatial perspective can have a profound influence on our interpretation of how logging affects bird communities and populations. The complex mosaic of the boreal forest cannot be studied as a series of habitats in isolation from one another. Bird species do not necessarily perceive the same habitat divisions as humans, and by analyzing all forested habitats I observed a much different pattern of species responses than with a patch-centred perspective. Neither can conclusions drawn at one small spatial scale be extrapolated to larger scales. Even with a small increase in scale (relative to northern Alberta) I observed a change in population and

community effects of fragmentation. Only with a careful definition of relevant habitats and an appropriate scale (or multiple scales) can the actual effects of forest fragmentation on songbirds be determined. I recommend future sampling of bird communities to be conducted with less reference to anthropocentrically-defined habitat patches such as are typically identified on timber harvesting maps. Larger scales of investigation should become a priority, perhaps by using bird atlas data or extensive collaboration and data sharing, to help put results obtained at smaller scales into a more regional context.

3.6 Acknowledgements

Eric Christensen and Pat Gallupe of Pearson Timberline Forestry Consultants provided equipment and support for the GPS work. John Brzustowski wrote the computer programs necessary for producing the accumulation curves. Thanks to Craig Machtans, Mark Dale, and Ellen MacDonald for reviewing a previous draft of this chapter. This study was supported financially by a Partnership Grant from the Canadian Forest Service and the Natural Sciences and Engineering Research Council of Canada, and by Alberta-Pacific Forest Industries, Inc.

3.7 Literature Cited

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., and Soluk, D.A. 1987. Ecological neighborhoods: Scaling environmental patterns. Oikos **49**:340-346.

Allen, T.F.H. and Starr, T.B. 1982. Hierarchy: Perspectives for ecological diversity. Univ. of Chicago Press: Chicago, IL.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos **71**:355-366.

Blake, J.G., Hanowski, J.M., Niemi, G.J., and Collins, P.T. 1994. Annual variation in bird populations of mixed conifer-northern hardwood forests. Condor **96**:381-399.

Blondel, H., Ferry, C., and Frochot, B. 1981. Point counts with unlimited distance. Studies in Avian Biology **6**:414-420.

Boecklen, W.J. 1986. Effects of habitat heterogeneity on the species-area relationships of forest birds. J. Biogeog. **13**:59-68.

Böhning-Gaese, K., Taper, M.L., and Brown, J.H. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conserv. Biol. 7:76-86.

Brittingham, M.C. and Temple, S.A. 1983. Have cowbirds caused forest songbirds to decline? BioScience **33**:31-35.

Carlile, D.W., Skalski, J.R., Batker, J.E., Thomas, J.M., and Cullinan, V.I. 1989. Determination of ecological scale. Landscape Ecol. **2**:203-213.

Connell, J.H. and Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. **121**:789-824.

Cotterill, S.E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Cumming, S.G., Burton, P.J., Prahacs, and Garland, M.R. 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: A simulation study. For. Ecol. Manage. **68**:281-302.

Dunning, J.B., Danielson, B.J., and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Forman, R.T.T., Galli, A.E., and Lack, C.F. 1976. Forest size and avian diversity in New Jersey with some land use implications. Oecologia **26**:1-8.

Freemark, K., and Merriam, H.G. 1986. The importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. **36**:115-141.

Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Butterworths: London, UK.

Haila, Y., Hanski, I.K., and Raivio, S. 1989. Methodology for studying the minimum habitat requirements of forest birds. Ann. Zool. Fennici **26**:173-180.

Hansen, A.J. and Urban, D.L. 1992. Avian response to landscape pattern: The role of species' life histories. Landscape Ecol. **3**:163-180.

Hansson, L. 1992. Landscape ecology of boreal forests. Trends Ecol. Evol. 7:299-302.

Hansson, L. and Angelstam, P. 1991. Landscape ecology as a theoretical basis for nature conservation. Landscape Ecol. **4**:191-201.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. **62**:447-502.

Hosmer, D.W., and Lemeshow, S. 1989. Applied logistic regression. J. Wiley & Sons: Toronto, ON. 307 pp.

Jackson, D.A., Somers, K.M., and Harvey, H.H. 1989. Similarity coefficients: Measures of co-occurrence and association or simply measures of occurrence? Am. Nat. **133**:436-453.

Knight, T.W. and Morris, D.W. 1996. How many habitats do landscapes contain? Ecology **77**:1756-1764.

Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology **74**:1659-1673.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Lord, J.M., and Norton, D.A. 1990. Scale and the spatial concept of fragmentation. Conserv. Biol. **4**:197-202.

Ludwig, J.A., and Reynolds, J.F. 1988. Statistical ecology: A primer on methods and computing. J. Wiley & Sons: Toronto, ON. 337 pp.

MacArthur, R.H., and Wilson, E.O. 1967. The theory of island biogeography. Princeton Univ. Press: Princeton, NJ. 203 pp.

Martin, T.E. 1992. Breeding Biology Research Database (BBIRD) program: General overview and standardized protocols. U.S. Dept. of the Interior, Fish and Wildlife Service, Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas, Fayetteville, AR.

Maurer, B.A. 1985. Avian community dynamics in desert grasslands: Observational scale and hierarchical structure. Ecol. Monogr. **55**:295-312.

McGarigal, K. and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. **65**:235-260.

Merriam, G. 1988. Landscape dynamics in farmland. Trends Ecol. Evol. **3**:16-20.

Montgomery, D.C. and Peck, E.A. 1982. Introduction to linear regression analysis. J. Wiley & Sons: New York, NY.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology **68**:362-369.

Morton, E.S. 1992. What do we know about the future of migrant landbirds? pp. 579-589 in: J.M. Hagan and D.W. Johnson, eds. *Ecology and management of Neotropical migrant landbirds*. Smithsonian Inst. Press: Washington D.C.

Norušis, M.J. 1994. SPSS Professional Statistics™ 6.1. SPSS Inc: Chicago, IL. 385 pp.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., and Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton Univ. Press: Princeton, NJ. 253 pp.

O'Neill, R.V., Milne, B.T., Turner, M.G., and Gardner, R.H. 1988. Resource utilization scales and landscape pattern. Landscape Ecol. **2**:63-69

Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., and DeSante, D.F. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. 41 pp.

Robbins, C.S., Sauer, J.R., Greenberg, R.S., and Droege, S. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. USA **86**:7658-7662.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: Conceptual issues and the evidence. Biol. J. Linn. Soc. **42**:149-163.

Rowe, J.S. 1972. Forest regions of Canada. Canadian Forest Service Publ. No. 1300. 172 pp.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: A review. Conserv. Biol. **5**:18-32.

Schieck, J., Nietfeld, M., and Stelfox, J.B. 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. Can. J. Zool. **73**:1417-1431.

Schmiegelow, F.K.A., Machtans, C.S., and Hannon, S.J. In press. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology.

Schneider, D.C. 1994. Quantitative ecology: Spatial and temporal scaling. Academic Press: Toronto, ON. 395 pp.

Semenchuk, G.P., ed. 1992. The atlas of breeding birds of Alberta. Federation of Alberta Naturalists, Edmonton, AB.

Smith, A. 1993. Ecological profiles of boreal forest birds in western and northern Canada. pp. 14-26 in: D. Kuhnke, ed. *Birds in the boreal forest: Proceedings of a workshop held March 10-12 in Prince Albert, SK.* Forestry Canada and Environment Canada, Edmonton, AB.

ter Braak, C.J.F. 1987. Ordination. pp. 61-173 in: R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren, eds. *Data analysis in community and landscape ecology.* PUDOC, Wageningen, The Netherlands.

ter Braak, C.J.F. 1988*a*. CANOCO - a FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis (Version 2.0). TNO Institute of Applied Computer Science, Wageningen, The Netherlands.

ter Braak, C.J.F. 1988*b*. CANOCO - an extension of DECORANA to analyse species-environment relationships. Vegetatio **75**:159-160.

ter Braak, C.J.F. 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group. Wageningen, The Netherlands.

ter Braak, C.J.F. and Looman, C.W.N. 1987. Regression. pp. 29-77 in: R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren, eds. *Data analysis in community and landscape ecology.* PUDOC, Wageningen, The Netherlands.

Turner, M.G. 1989. Landscape ecology: The effect of pattern on process. Ann. Rev. Ecol. Syst. **20**:171-197.

Trimble Navigation Ltd. 1992. Trimble PFINDER software user's guide, Rev. C, Version 2.3. Sunnyvale, CA.

Villard, M-A., Freemark, K., and Merriam, G. 1992. Metapopulation theory and neotropical migrant birds in temperate forests: An empirical investigation. pp. 474-482 in: J.M. Hagan and D.W. Johnson, eds. *Ecology and management of Neotropical migrant landbirds.* Smithsonian Inst. Press: Washington D.C.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: A multi-scale approach. Oikos **62**:59-66.

Welsh, D.A. and Lougheed, S.C. 1996. Relationships of bird community structure and

species distributions to two environmental gradients in the northern boreal forest. Ecography **19**:194-208.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimliewcz, M.K., and Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. pp. 125-205. in: R.L. Burgess and D.M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag: New York, NY.

Wiens, J.A. 1989*a*. Spatial scaling in ecology. Functional Ecol. **3**:383-397.

Wiens, J.A. 1989*b*. The ecology of bird communities. Volume 2. Processes and variations. Cambridge Univ. Press: Cambridge, UK. 316 pp.

Wiens, J.A. 1994. Habitat fragmentation: Island *v* landscape perspectives on bird conservation. Ibis **137**:S97-S104.

Wiens, J.A., Rotenberry, J.T., and Van Horne, B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. Oikos **48**:132-147.

Wilcove, D.S., McLellan, C.H., and Dobson, A.P. 1986. Habitat fragmentation in the temperate zone. pp. 237-256 in: M.E. Soulé, ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Assoc. Inc.: Sunderland, MA.

CHAPTER 4

Thesis Discussion

4.1 Summary of Results

In this thesis I examined two topics related to the impacts on songbirds of clearcut logging and associated landscape fragmentation. I looked at a site-level question of how songbirds respond to partial-cut logging in contrast to clearcut logging, and thereby considered the utility of partial-cutting in ameliorating the effects of logging on songbirds. I also investigated broad landscape-level phenomena associated with concepts of spatial scale and landscape perspective. These were examined in the context of their potential influences on the findings of other studies conducted in fragmented landscapes that have typically been conducted at smaller spatial scales and focussed on one particular habitat.

In Chapter 2 I found that vegetation structure retained by a partial-cut harvesting strategy can help maintain bird populations and communities closer to pre-cut conditions than clearcutting. While some species were lost, and many declined in numbers, partial-cuts did retain most species present before harvesting. The number of species present on a cutblock and the abundance of individuals were both correlated with the amount of vegetation cover removed during harvesting. Partial-cut logging thus appeared to reduce the impact of forestry on songbirds, although I limited that conclusion to the small scale and over the short term.

In Chapter 3 I presented results that indicated that both a wider landscape view, and a larger scale of sampling can affect our interpretations of songbird response to fragmentation, compared to small-scale and single habitat studies. The apparent response to fragmentation of several species depended on what habitats were included in the analysis, or at what scale sampling was conducted. The evidence suggested that there was no inherent scale in bird communities within the range of scales I examined. There was also some suggestion that the spatial structure of bird communities was different in the logged landscape. All of this pointed towards the importance of including landscape and large scale factors in future research, and to the hazards of extrapolating studies of restricted scope to broad scale management recommendations.

4.2 Directions for Future Research

4.2.1 Partial-Cut Logging

Several caveats with regards to the results of the study presented in this thesis have already been offered (§ 2.4.3). Many of these directly suggest further research that could be initiated in order to obtain a more complete picture of the apparent benefits of partial-cut logging.[1] Firstly, the single-year of post-cutting data that I collected should be extended. Population trends may become significant over the longer term. Also, the year-to-year variation in the different treatments needs to be addressed, as it is possible that some of the species recorded as present in some cutblocks may not be consistent in their use of these areas across years. The great increase in bird species richness and abundance in control sites post-cutting complicated the interpretation of numbers from harvested blocks. Personal observations in the field also suggested that, for some species, partially-cut areas might have functioned as foraging habitat, but not nesting habitat. The behaviour of birds around the edges of partial-cuts should be compared to clearcuts.

The impacts of different harvesting strategies on the regeneration of aspen is of critical importance as well. Partial-cutting may be a poor option when considering timber growth because partial-cuts may exhibit reduced growth of aspen suckers, compared to growth rates in clearcuts, due to increased shading (Peterson and Peterson 1992). In contrast, bird communities may return to pre-harvest conditions more quickly under a partial-cut prescription because of the increased vegetation structure. A further feature of current logging practices of potential concern to songbirds is the selective elimination of mixed stands of aspen and white spruce (Cumming *et al.* 1994). It is possible that higher shading on partial-cuts might promote the growth of white spruce, and thus help avoid the problem of "unmixing the mixedwood" . Given adequate funding, aspen regeneration should be monitored so the interactions between vegetation cover, timber growth potential, and bird use of cutblocks can be investigated.

Small mammals are known to be responsible for a large proportion of nest

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[1] In fact, many of these are currently being investigated on the same sites as used in my study. Contact Rebecca Tittler, Department of Biological Sciences, University of Alberta, Edmonton, AB.

predation occurring in boreal forests (Cotterill 1996). The response of small mammals to partial-cut logging is not known, but a simple live-trapping program could easily allow a rough determination. Avian predators, including raptors, corvids and House Wren, and the nest parasitic Brown-Headed Cowbird would be adequately censused with continued bird community surveys. A nest predation experiment would likely not be an efficient expenditure of resources, unless it is determined that predator communities do in fact differ between treatments.

4.2.2 Landscape and Scale Effects

The most immediate need suggested by the results presented in Chapter 3 is to continue to attempt to identify an inherent scale within boreal songbird communities. The curves of cumulative species richness and turnover generally did not reach a horizontal asymptote over the scale range I examined. The identification of inherent scale is of fundamental importance to further community ecological studies to ensure that suggestions of processes are being drawn from a relevant pattern. There is no guarantee that boreal bird communities actually possess such an inherent scale. This will depend in part on the nature of spatial patterning of vegetation communities and physical environmental variables, the variances of the latter of which have, at least in some cases, shown to increase continually with scale (Bell *et al.* 1993). Cumming *et al.* (1996) have found that at no spatial scale can a representative region, in terms of stand age and size structures, of the boreal mixedwood be found. For birds, data sets already exist that could expand the scale of investigation to the level of roughly four townships (approximately 400 km^2) if data were pooled from other studies in the Calling Lake area.

Also of interest is the manner in which the 'landscape effect' operates. From my study it is clear that a consideration of multiple landscape habitat components can significantly alter our interpretation of fragmentation processes. My data are limited in their ability to suggest process, though, because of a lack of pre-harvest data and the low resolution of point-count census data. A combination of a before-and-after-treatment experimental design (Wiens and Parker 1995) and territory mapping of birds in aspen and mixed forest stands, without regard to stand boundaries, would help to distinguish

between possible processes. Are 'landscape effects' connected simply with a more complete census of some bird species' habitats? Or is there a process of habitat compensation occurring whereby species being displaced by logging are able to, in a sense, substitute other forest types for their 'preferred' habitats? What are the fitness consequences of such an occurrence? These are big questions which will require both a high intensity and a large scale of investigation.

4.3 Multiple Scales of Forest Management

The studies I have presented in this thesis are only a small part of the large amount of research currently being conducted in Alberta's boreal forest. Several other studies have been, and are continuing to be conducted in the Calling Lake area, and two large forest research programs are operating out of the University of Alberta: the TROLS buffer strip project, and the Network of Centres of Excellence in Sustainable Forest Management[2]. As data from these various studies become available, a much more comprehensive set of recommendations for forest management will be possible. I would like to offer only a few general comments on the topic to conclude my work in the applied context in which it was initiated.

Forest management plans have always implicitly operated over a hierarchy of spatial scales. At a minimum, guidelines for cutblock design and harvesting technique have been a component of plans with a specified Annual Allowable Cut within some designated area of forest. Certainly, many management plans contained little more than this in the not-so-distant past. More recently, calls for a more ecologically sound method of harvesting forests have been widely heard. One of the recurring themes in these recommendations has been the need for a better integration of multiple spatial scales in management planning, particularly recognizing the importance of the large scale (*e.g.* Noss 1983, Petit *et al.* 1995). The importance of multiple scales of research and planning can be seen as an underlying theme of this thesis as well.

Site-specific management has received far more attention historically, for it is at

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[2] For further information contact Dr. Susan Hannon, Department of Biological Sciences, University of Alberta, Edmonton, AB.

this scale that logging is actually accomplished. Structures and patterns in forests at a small-scale do play a key role in determining wildlife associations. Management goals for particular species or guilds are sometimes best achieved with small scale planning. For instance, the maintenance of a cavity nesting guild can be achieved with the retention of standing dead trees on cutblocks. Retention of increased vertical structure can help maintain higher local diversity of birds (Hunter 1990). A range of different silvicultural prescriptions can be used across a managed landscape to attain a variety of these sorts of goals.

Conservation is, almost by definition, a large scale issue, and particular sites can not be considered in isolation from the surrounding landscape and regional context. An understanding of how birds use the entire landscape is critical, such that an aspen cutblock surrounded by spruce may require different mangement than an aspen cutblock surrounded by more aspen. Similarly, knowledge about the scales at which natural communities operate, and the scales at which forestry may affect those communities should play a role in designing regional management plans. This becomes especially important when other species of wildlife, which may operate at very different scales, are brought into the picture. Thus it is appropriate to investigate the effects of partial-cutting at the small scale of individual cutblocks (although partial-cuts may affect larger scale processes as well), but landscape-scale alteration of forests such as fragmentation must be dealt with at larger scales. Better understanding of the dynamics of bird populations and communities at large scales is necessary to effectively design large scale elements of a management plan (*e.g.* landscape connectivity, stand age distributions).

I have presented data related to both site specific and landscape-level forest management issues. While the linkage between the two may not be obvious from an academic-scientific perspective, the linkage in terms of a hierarchical management scenario is clear. There is no single scale at which management can appropriately be conducted (Christensen *et al.* 1996), and monitoring the effects of various management strategies must also be conducted at multiple scales in space and time (Noss 1990). Thus small scales of management might be appropriate for the conservation of a particular species (or

similarly for the utilization of a particular resource), while maintenance of such inherently large-scale concepts as biodiversity, ecological integrity, or Annual Allowable Cut require much larger scales of focus, vagueness of definitions notwithstanding. For traditionally trained scientists, a requirement to conduct research and apply their findings at large scales brings with it tough challenges:

> Scientists are often not well adapated to the time and space limits of policy analyses....The large spatial scales of a problem often limit the amount of detail that can be incorporated in an analysis; scientists trained in a reductionist mode may find it difficult to leave behind this detail.
>
> (Franklin 1995)

The integration of large and small scales is especially challenging because, relatively speaking, so much is known about the small scale, and so little is known about the large. To me, this simply suggests the need for continued research effort at large scales, while building in increasing margins of error with increasing scale of management.

4.4 Literature Cited

Bell, G., Lechowicz, M.J., Appenzeller, A., Chandler, M., DeBlois, E., Jackson, L., Mackenzie, B., Preziosi, R., Schallenberg, M., and Tinker, N. 1993. The spatial structure of the physical environment. Oecologia **96**:114-121.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., and Woodmansee, R.G. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecol. Appl. **6**:665-691.

Cotterill, S.E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Cumming, S.G., Burton, P.J., Prahacs, S., and Garland, M.R. 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: A simulation study. For. Ecol. Manage. **68**:281-302.

Cumming, S.G., Burton, P.J., and Klinkenberg, B. 1996. Boreal mixedwood forests may have no "representative" areas: Some implications for reserve design. Ecography

19:162-180.

Franklin, J.F. 1995. Scientists in Wonderland. BioScience 45:S74-S78.

Hunter, M.L. 1990. Wildlife, forests, and forestry. Prentice Hall: Englewood Cliffs, NJ. 370 pp.

Noss, R.F. 1983. A regional landscape approach to maintain diversity. BioScience 33:700-706.

Noss, R.F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. Conserv. Biol. 4:355-364.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, AB. Special Report 1. 252 pp.

Petit, L.J., Petit, D.R., and Martin, T.E. 1995. Landscape-level management of migratory birds: looking past the trees to see the forest. Wildl. Soc. Bull. 23:420-429.

Wiens, J.A. and Parker, K.R. 1995. Analyzing the effects of accidental environmental impacts: Approaches and assumptions. Ecol. Appl. 5:1069-1083.

APPENDIX 1

Spatial Structure of Bird Communities.

Introduction

In addition to a simple consideration of the importance of the scale of investigation, such as presented in Chapter 3, is the potential importance of the spatial arrangement of the sampling locations in space. Biotic communities are not spatially homogeneous, but exhibit various types of spatial structure (Legendre and Fortin 1989). This can be of interest in its own right for the role it may play in ecosystems, or to assess the degree to which other analyses of the same data may be confounded by spatial autocorrelation (Legendre 1993). Of interest here was the notion that if birds became more patchily distributed following forest fragmentation, the matrix of bird species data would exhibit more spatial variation, independent of vegetation variation, in the fragmented landscape than in the unlogged landscape.

Spatial structures can be detected by recent advances in techniques of canonical ordination (ter Braak 1986, 1987). Ordination is used in place of multiple regression when an entire matrix is to be considered as a whole; the canonical form incorporates supplied descriptor variables into the ordination and eliminates *ex post facto* correlation analyses. Such ordination analyses allow measurement of the fraction of the variation in a species matrix explained by a set of environmental variables alone, or the spatial structure of the species data alone, or the total explanatory power of both data sets simultaneously (Borcard *et al.* 1992). This technique performs a series of partial constrained ordinations by removing the effects of covariables on the analyzed data set by multiple linear regression.

Methods

The matrix of bird species abundances was related simultaneously to corresponding matrices of vegetation characteristics and geographical coordinates. The logged and control landscapes were analyzed separately; all sampling locations from aspen patches in each landscape were used in the analysis. Census stations were arranged over roughly 7000 ha in each landscape (for details see § 3.2.3.3). Bird communities were

sampled using a point-count technique (§ 2.2.3) and local vegetation was measured at each station (§ 2.2.2). A matrix of geographical coordinates (derived from Geographic Positioning System data) was completed by adding all terms for a cubic trend surface regression (Borcard *et al.* 1992). Thus, the total variation of the bird species data was partitioned as follows (Borcard *et al.* 1992):

a) the nonspatial environmental variation which was the fraction of the variation in the bird data that could be explained by vegetation characteristics independently of any spatial structure;

b) the spatial structuring in the bird data that was shared by the vegetation data;

c) the spatial structuring in the bird data that was not shared by the vegetation data;

d) the fraction of the bird species variation which could not be explained by geographical coordinates nor by the supplied vegetation data.

The three data matrices were analyzed simultaneously by a series of partially-constrained ordinations. A preliminary Detrended Correspondence Analysis indicated that a linear model of bird species' responses to environmental gradients was appropriate. This made intuitive sense given the narrow range of habitats included in the analysis. Redundancy Analysis (van den Wollenberg 1977) was selected for further analyses as a direct ordination technique based on a linear model. Significant terms from the spatial matrix were selected using a forward selection procedure and α=0.05. The ordination was performed twice, the first with the full suite of 29 vegetation variables, the second retaining only one member of highly correlated sets of variables, as assessed by Variable Inflation Factors (*i.e.* omitting variables with VIF>20, ter Braak [1988*a*]). The analysis was performed using CANOCO version 3.12 software (ter Braak 1988*a*,*b*, 1990).

Results

Bird community structure was predicted only slightly by a matrix of spatial relationships of the sampling locations (Table A1-1). The spatial matrix accounted for more variation of the bird data in the logged landscape, and only in the logged landscape

was the 'spatial' canonical axis statistically significant after removing vegetation influences (Monte Carlo randomization test; logged $p = 0.02$; control $p = 0.73$). Explained variances were very low for both landscapes, however. In both, local vegetation structure explained the largest portion of the variance in the species matrix. Almost half the total variation in both landscapes remained 'unexplained' by both the vegetation and geographical coordinates matrices.

Different sets of spatial variables were found to be significant in the two landscapes. In the logged landscape, higher order combinations of the geographical coordinates were selected (eq. 1), but not in the control landscape (eq. 2).

$$\hat{z}_l = b_1x + b_2y + b_3y^2 + b_4x^2y \qquad \text{(eq. 1)}$$

$$\hat{z}_c = b_1x + b_2y \qquad \text{(eq. 2)}$$

Table A1-1: Variance partitioning of bird community data in logged and unlogged (reference) landscapes.

Variance component	Explained Variance (%)	
	Logged landscape	Reference landscape
Non-spatial vegetational	39.2	43.3
Spatial plus vegetational	8.0	3.1
Spatial non-vegetational	9.3	2.2
Unexplained	43.5	51.4

Discussion

Given the increasing focus of ecological research into spatial phenomena, it is important to address the fact that many, if not most, ecological data exhibit some degree of spatial autocorrelation. In cases where there is a high degree of shared spatial structure between the species of interest and some measured environmental variables, the importance of the environmental variables can be overestimated, and the true contribution

of spatial relationships of samples masked (Legendre 1993).

As predicted, the bird community in the logged landscape exhibited a greater degree of spatial structuring than that in the control landscape. One strength of the analytical technique used here is that by including second and third order combinations of geographic coordinates, larger scale and more complex spatial structures are detected than would be with only simple x and y coordinates. There is evidence that bird communities in the logged landscape exhibit such complex structuring as shown by the selection of 4 terms from the spatial matrix. Landscape fragmentation appears to have induced a large scale, but subtle, change in bird communities. It is not clear what role such spatial structure might play, but since heterogeneity is frequently of functional importance (Legendre and Fortin 1989) it warrants further consideration.

Considering the level of detail contained in the vegetation matrix, the amount of unexplained variation seems a little surprising. A myriad biological factors may be responsible for the remaining structure (*e.g.*dispersal ability), but at this point it is not possible to distinguish between the 'potentially explainable' and the true stochasticity in the data set (Borcard *et al.* 1992). A further important step is this analysis would be to include variables describing landscape structure on a larger scale, because these factors have been shown to be important to birds at the population level elsewhere (Pearson 1993, McGarigal and McComb 1995). Including these data as a fourth matrix would not be a simple task as methods for analyzing four matrices simultaneously do not yet exist.

This fairly cursory analysis presents further evidence for landscape fragmentation affecting bird communities. If the trend suggested here is 'real', then communities may be responding in subtle but large-scale ways that have not been thoroughly investigated before. This emphasizes the need for large, landscape-scale analyses of how bird communities are affected by fragmentation.

Acknowledgement

Thanks to Jim Schieck for his comments on this section, provided on very short notice.

Literature Cited

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology **73**:1045-1055.

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology **74**:1659-1673.

Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107-138.

McGarigal, K. and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. **65**:235-260.

Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. **8**:3-18.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

_____. 1987. Ordination. pp. 61-173 in: R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren, eds. *Data analysis in community and landscape ecology*. PUDOC, Wageningen, The Netherlands.

_____. 1988*a*. CANOCO - a FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis (Version 2.0). TNO Institute of Applied Computer Science, Wageningen, The Netherlands.

_____. 1988*b*. CANOCO - an extension of DECORANA to analyse species-environment relationships. Vegetatio **75**:159-160.

_____. 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group. Wageningen, The Netherlands.

van den Wollenberg, A.L. 1977. Redundancy analysis: An alternative for canonical correlation analysis. Psychometrica **42**:207-219.

APPENDIX 2

Bird species names and relative abundances.

Woodpeckers (Picidae) and songbirds (Passeriformes) detected during point-count surveys for Chapter 3, with the migratory strategy of each species. The total number of detections of each species across all sites in each landscape in 1994 and 1995 combined is given; the list is sorted by frequency of detection in the reference landscape.

Common Name	Scientific Name	Migratory Status[a]	Total Detections[b] (1994 & 1995)	
			Control	Logged
Ovenbird	*Seiurus aurocapillus*	NTM	486	427
White-Throated Sparrow	*Zonotrichia albicollis*	SDM	388	352
Red-Eyed Vireo	*Vireo olivaceus*	NTM	382	240
Yellow-Rumped Warbler	*Dendroica coronata*	SDM	326	378
Mourning Warbler	*Oporornis philadelphia*	NTM	246	109
Connecticut Warbler	*Oporornis agilis*	NTM	212	181
Tennessee Warbler	*Vermivora peregrina*	NTM	172	85
Least Flycatcher	*Empidonax minimus*	NTM	161	97
Swainson's Thrush	*Catharus ustulatus*	NTM	110	122
Chipping Sparrow	*Spizella passerina*	NTM	102	198
American Redstart	*Setophaga ruticilla*	NTM	72	16
Western Tanager	*Piranga ludoviciana*	NTM	61	71
Red-Breasted Nuthatch	*Sitta canadensis*	R	60	61
Black-Thr. Green Warbler	*Dendroica virens*	NTM	59	57
Yellow-Bellied Sapsucker	*Sphyrapicus varius*	SDM	54	66
Rose-Breasted Grosbeak	*Pheucticus ludovicianus*	NTM	50	17
Gray Jay	*Perisoreus canadensis*	R	44	75
Winter Wren	*Troglodytes troglodytes*	SDM	43	39
Yellow Warbler	*Dendroica petechia*	NTM	38	22
Solitary Vireo	*Vireo solitarius*	SDM	33	27
Hermit Thrush	*Catharus guttatus*	SDM	30	43

Common Name	Scientific Name	Migratory Status[a]	Total Detections[b] (1994 & 1995)	
			Control	Logged
Golden-Crowned Kinglet	*Regulus satrapa*	SDM	28	16
Brown Creeper	*Certhia americana*	R	28	15
Ruby-Crowned Kinglet	*Regulus calendula*	SDM	21	19
Black-Capped Chickadee	*Parus atricapillus*	R	18	34
Black-and-White Warbler	*Mniotilta varia*	NTM	18	3
Warbling Vireo	*Vireo gilvus*	NTM	17	12
Northern Flicker	*Colaptes auratus*	SDM	12	11
Lincoln's Sparrow	*Melospiza lincolnii*	NTM	11	72
Dark-Eyed Junco	*Junco hyemalis*	SDM	7	40
Bay-Breasted Warbler	*Dendroica castanea*	NTM	7	4
Boreal Chickadee	*Parus hudsonicus*	R	6	8
Hairy Woodpecker	*Picoides villosus*	R	6	8
American Robin	*Turdus migratorius*	SDM	5	7
Downy Woodpecker	*Picoides pubescens*	R	4	1
Pine Siskin	*Carduelis pinus*	SDM	4	P
Canada Warbler	*Wilsonia canadensis*	NTM	3	2
Cape May Warbler	*Dendroica tigrina*	NTM	3	2
Magnolia Warbler	*Dendroica magnolia*	NTM	2	4
Three-Toed Woodpecker	*Picoides tridactylus*	R	2	2
Orange-Crowned Warbler	*Vermivora celata*	SDM	2	2
White-Winged Crossbill	*Loxia leucopiera*	R	2	P
Cedar Waxwing	*Bombycilla cedrorum*	SDM	1	13
Common Yellowthroat	*Geothlypis trichas*	NTM	1	P
Blackpoll Warbler	*Dendroica striata*	NTM	1	
Clay-Coloured Sparrow	*Spizella pallida*	NTM		9
Song Sparrow	*Melospiza melodia*	SDM		8
Brown-Headed Cowbird	*Molothrus ater*	SDM		7

Common Name	Scientific Name	Migratory Status[a]	Total Detections[b] (1994 & 1995)	
			Control	Logged
Western Wood-Pewee	*Contopus sordidulus*	NTM		5
Alder Flycatcher	*Empidonax alnorum*	NTM	P	4
Purple Finch	*Carpodacus purpureus*	SDM		3
House Wren	*Troglodytes aedon*	SDM		3
Eastern Phoebe	*Sayornis phoebe*	SDM		3
Tree Swallow	*Iridoprocne bicolor*	SDM	P	3
Blue Jay	*Cyanocitta cristata*	R	P	2
LeConte's Sparrow	*Ammospiza leconteii*	SDM		2
Pileated Woodpecker	*Dryocopus pileatus*	R	P	2
Swamp Sparrow	*Melospiza georgiana*	SDM		1
Northern Oriole	*Icterus galbula*	NTM		1
Palm Warbler	*Dendroica palmarum*	NTM	P	1
Philadelphia Vireo	*Vireo philadelphicus*	NTM		1
Olive-Sided Flycatcher	*Nuttalornis borealis*	NTM	P	P
Common Raven	*Corvus corax*	R	P	P
Red-Winged Blackbird	*Agelaius phoeniceus*	SDM	P	P
Evening Grosbeak	*Hesperiphona vespertina*	SDM		P
American Crow	*Corvus brachyrhynchos*	SDM		P
Common Grackle	*Quiscalus quiscula*	SDM		P

[a] R, resident year-round; SDM, short-distance migrant; NTM, neotropical migrant.
[b] 'P' denotes species known to be present but not detected within 100 m radius, or only detected flying over.

APPENDIX 3

Summaries of Vegetation Regressions from § 3.2.3.3.

Variable names used in model expressions:

`CT` - Coniferous trees
`PT` - *Populus balsamifera* trees
`AWT` - *Alnus* spp. & *Salix* spp. trees
`CSap` - Coniferous saplings
`PSap` - *Populus* spp. saplings
`AWSap` - *Alnus* spp. & *Salix* spp. saplings
`OSap` - Other saplings
`SSnag` - Small snags (8-12 cm dbh)
`LSnag` - Large snags (>12 cm dbh)
`CHt` - Canopy height (m)
`SCHt` - Subcanopy height (m)
`CCov` - Canopy cover (%)

• Stepwise linear regression models of vegetation on *species richness* for all aspen sites in both landscapes. Correlation coefficient, test statistic, and associated probability are given.

1994

$$\hat{y} = 7.827 + 0.339\texttt{PT} + 0.370\texttt{AWSap} - 0.322\texttt{OSap}$$

adj. $r^2 = 0.117$
F ratio = 5.85, $p = 0.001$

1995

$$\hat{y} = 6.870 + 0.396\texttt{AWT} - 0.403\texttt{LSnag} - 0.261\texttt{CSap} - 0.349\texttt{SSnag}$$

adj. $r^2 = 0.154$
F ratio = 7.09, $p < 0.001$

• Stepwise linear regression models of vegetation on *total bird abundance* for all aspen sites in both landscapes. Correlation coefficient, test statistic, and associated probability are given.

1994

$$\hat{y} = 11.505 - 1.006\texttt{CSap} - 0.396\texttt{OSap} - 0.858\texttt{SSnag} - 0.614\texttt{SCHt}$$

adj. $r^2 = 0.237$
F ratio = 9.53, $p < 0.001$

1995

$$\hat{y} = 8.958 + 0.661\text{AWT} - 0.635\text{CT} - 0.662\text{LSnag} - 0.582\text{SSnag}$$

adj. $r^2 = 0.246$
F ratio = 11.93, $p < 0.001$

• Stepwise logistic regression models of vegetation on *species presence/absence* for all aspen sites in both landscapes, where the probability of a species occurrence is given by $1/(1 + e^{-Z})$. Variables in *italics* were recoded to categorical values (low, high) prior to analysis. Model success is given as the percentage of observations correctly classified (presence, absence). Overall model test statistic (χ^2) and associated probability are given.

Least Flycatcher

$$Z = 6.046 - 0.885\textit{CT} - 4.157\textit{CSap} + 0.952\text{SSnag}$$

% correct (36.0, 94.4)
$\chi^2 = 34.05$, $p < 0.001$

Swainson's Thrush

$$Z = 0.715 + 0.511\textit{CT} + 0.502\text{LSnag} + 0.447\text{CCov}$$

% correct (26.3, 91.4)
$\chi^2 = 15.37$, $p = 0.002$

Red-Eyed Vireo

$$Z = -0.796 - 1.555\textit{CT} - 1.250\text{Sap} - 0.545\text{CHt}$$

% correct (69.8, 46.4)
$\chi^2 = 5.94$, $p = 0.015$

Yellow-Rumped Warbler

$$Z = 0.040 + 0.894\textit{CT}$$

% correct (54.9, 83.1)
$\chi^2 = 18.81$, $p < 0.001$

Tennessee Warbler

$$Z = -0.421 + 0.560AWT$$

% correct (37.5, 83.6)
$\chi^2 = 6.81, p = 0.009$

Connecticut Warbler

$$Z = -0.352 - 1.786SSnag - 1.027PT - 0.597AWT - 0.976CSap$$

% correct (85.5, 55.3)
$\chi^2 = 48.39, p < 0.001$

Mourning Warbler

$$Z = 0.170 - 1.281CT + 0.838SSnag + 0.627CCov - 1.257CHt - 0.490PSap$$

% correct (80.3, 74.0)
$\chi^2 = 61.02, p < 0.001$

Ovenbird

$$Z = -0.177 + 0.665CT - 0.437OSap + 0.659AWSap - 0.437PT$$

% correct (71.7, 67.8)
$\chi^2 = 27.88, p < 0.001$

White-Throated Sparrow

$$Z = -0.094 + 0.472SSnag$$

% correct (69.8, 46.4)
$\chi^2 = 5.94, p = 0.015$

Chipping Sparrow

$$Z = 0.693 + 2.023CT + 0.519OSap + 0.569CHt + 1.667PSap$$

% correct (44.8, 96.5)
$\chi^2 = 35.90, p < 0.001$